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The Distribution of the Planktonic Chaetognatha in the Pacific and their Relationship to the Water Masses[1]

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ABSTRACT

The geographic extents of 27 species of Chaetognatha in the Pacific have been inferred from analyses of 2,900 plankton samples taken at more than 900 stations.

Two species of chaetognaths—*Sagitta elegans* and *S. maxima*—are found in the Pacific only in the Subarctic Water Mass. Four species—*Sagitta enflata, S. hexaptera, S. pacifica,* and *Pterosagitta draco*—occur in the Pacific Equatorial and Central Water Masses. Seven species—*Sagitta robusta, S. regularis, S. ferox, Krohnitta pacifica, Sagitta bedoti, S. neglecta,* and *S. pulchra*—occur in the Equatorial and Western Central Water Masses. The latter three species appear to be disjunct equatorial species that are absent from the central equatorial Pacific. *Sagitta pseudoserratodentata* occupies the North Pacific Central Water Mass. *S. californica,* essentially a warm-water cosmopolite, is very rare in the Equatorial Water Mass. The Peru and California Currents are inhabited by *Sagitta friderici.* A close relative, *S. crassa,* lives in the coastal waters of Japan. *Sagitta minima, Sagitta* species (*serratodentata* group), *Sagitta decipiens, S. lyra,* and *Krohnitta subtilis,* species which have their maximum abundance at about 200 meters (somewhat deeper than all of the preceding), appear to be limited in the north at about 45° N. Lat. *Sagitta planctonis, S. macrocephala,* and *Eukrohnia fowleri,* living primarily at depths of 500 meters and greater, have been taken in the present study as far north as 55° N. Lat., both in the Bering Sea and Gulf of Alaska. The very deep living species, *Heterokrohnia mirabilis,* was taken at a single station in the Eastern Equatorial Pacific. The sharpest chaetognath boundary yet found in the Pacific occurs in the Eastern Pacific at 18° to 20° N. Lat. and is associated with pronounced temperature, oxygen, and probably salinity gradients.

Species distributions analogous to those of the Chaetognatha are found in the euphausiids, copepods, and dinoflagellates among other groups of organisms.

INTRODUCTION

Since the first chaetognath was described in 1778 by the Dutch worker, Martin Slabber, more than five-hundred papers have been published that deal wholly or in part with this group of marine animals. In the past 25 years there has been a considerable increase in the amount of work on the Chaetognatha. This accelerated interest is due chiefly to a series of papers published by F. S. Russell between 1932 and 1939, in which he related the distribution of *Sagitta elegans* and *S. setosa* to good and poor years of herring spawning in the vicinity of the English Channel. Russell emphasized the use of chaetognaths as current indicators in that region, although the relationship of *S. elegans* and *S. setosa* to the water masses around England was set forth in an earlier work (Meek 1928) to which Russell did not refer.

The concept of using pelagic animals and the larvae of benthic organisms as indicators of water movement is at least as old as the era of the Challenger Expedition. For example, Agassiz (1883), writing of the

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pelagic coelenterates *Porpita*, *Velella*, and *Physalia*, said, "In fact these surface animals are excellent guides to the course of the current of the Gulf Stream,—natural current bottles, as it were." Fraser (1952) summarized some of the advantages as well as some of the problems of the modern work in this field. However, it must be admitted that indicator work is still largely based on qualitative methods and intuitive interpretations. There are as yet no formalized procedures or general agreement on techniques.

At the present time at least 24 scientists in ten countries, nearly three-fourths of them employed by government fishery research institutions, are working primarily on the Chaetognatha. Despite the comparatively large literature that has accumulated and the recent increase in interest in the group, it is not possible today to describe with any degree of confidence the limits or range in any ocean of more than one or two of the more than 40 known species. In view of the fact that indicator studies are based largely on variations in the geographic borders or limits of species, it is evident that such work is still in its infancy. The present study is a beginning at filling part of this void in our knowledge of the Chaetognatha in the Pacific.

From 1950 through 1955 the author examined the chaetognaths taken in plankton samples collected during more than 35 expeditions and routine marine life surveys in the North Pacific, in the equatorial regions of the South Pacific, and in the Beaufort-Chukchi Sea region of the Arctic. In the reduction and analysis of the accumulated data, it became evident that the findings for local areas could be properly interpreted only when compared to the findings for neighboring regions. Consequently, before publishing the detailed results from local regions, an overall picture of the distribution of the various species was worked out, insofar as the data and the published findings of other workers permitted. This general treatment is presented herein.

The author wishes to extend his sincere thanks to Professor Martin W. Johnson of the Scripps Institution, for his continued interest in and support of the author's research. I also wish to thank Drs. Thomas E. Bowman, Brian P. Boden, and Warren S. Wooster for their stimulating help in the beginning phases of this study. Discussions with Dr. Bowman, and Messrs. Edward Brinton, John S. Bradshaw, John A. McGowan, and Leo D. Berner, comparing their findings on other zooplankton groups with the Chaetognatha have been particularly helpful. Dr. Martin W. Johnson, Dr. Carl L. Hubbs, Mr. Stacey D. Hicks, Dr. E. Lowe Pierce, Dr. Takasi Tokioka, Dr. Fred B. Phleger, Dr. Robert S. Arthur, Dr. Joel W. Hedgpeth, and Dr. Norris W. Rakestraw made many helpful suggestions in reviewiig the manuscript. Mr. Townsend Cromwell kindly supplied the physical-chemical data from which Figures 24–26 were prepared.

This research was partially supported by the California Cooperative Oceanic Fisheries Investigations. One cannot adequately thank all those who took part in the difficult and at times hazardous task of collecting the samples which are the basis of this report.

PREVIOUS WORK IN THE PACIFIC

Four papers (Michael 1911; Tokioka 1939a, 1940a; Thomson 1947) stand out as the major contributions to our knowledge of the Chaetognatha in the Pacific. Thomson listed the papers on chaetognaths applicable to the geographic regions of the Pacific, to 1947. Some papers which he overlooked are the following. Baldasseroni (1915) reported on the species found on a trip from Valparaiso to Panama to Sydney, and Grey (1931) listed some chaetognath species from the Society Islands. Bigelow and Leslie (1930), in describing the hydrography and plankton in Monterey Bay, give the occurrence of several chaetognath species there. Papers by Dakin and Colefax (1940), Schilp (1941), Hsü (1943), and Mawson (1944) list various species of chaetognaths found in the western Pacific. Wailes (1929) first reported on the Chaetognatha from British Columbia. Although listed in Thomson's bibliography, papers by Russell (1934) and Grey (1922) are not included in his geographic summary.

Since Thomson's 1947 work, Tokioka has published several papers (1951, 1954a, 1954b, 1955a, 1955b, and 1956) dealing primarily with the occurrence of the Chaetognatha in the western Pacific, and Lea (1955) has added to our knowledge of the chaetognaths off British Columbia. Tchindonova (1955) has reported on the chaetognaths from the Kurile-Kamchatka Trench, and Bieri (1957) has given the first indication of the species to be found in the southeast Pacific. Other recent papers are those of Kusmorskaya (1949), Sproston (1949), Uyeno (1952), Maurice (1953), Thomson (1954), Hamon (1956), and Hida (1957).

MATERIAL

The 2,900 plankton samples that form the basis of this report were collected from more than 950 stations, mostly on cruises of the ships of the Scripps Institution of Oceanography, of the University of California. Many of the cruises were an integral part of the Marine Life Research Program of the California Cooperative Oceanic Fisheries Investigations. These extensive investigations off the California Coast were supplemented by a series of longer-ranging expeditions carried out by the Scripps Institution. In addition, many samples collected on vessels of the United States Navy and by the Pacific Oceanic Fisheries Investigations of the United States Fish and Wildlife Service were examined (Table 1 and Fig. 1).

Of the more than 950 stations involved, 720 are located by dots on the species distribution charts that follow. Stations off Baja California, California, Oregon, in the

TABLE 1. *Plankton samples analyzed for chaetognath species*

Expedition	Depth of tow in meters	No. of one-meter net samples	No. of trawls	No. other plankton samples
Mid-Pacific 1950	0–100,0–1000	6	28	38
Northern Holiday 1951	0–200	55	21	
Shellback 1952	0–300	203	18	
Long Line 1953	0–300	26		
Capricorn 1953	0–140	33		
Transpacific 1953	0–150,150–300,300–450, 450–600,0–1000	333		
Troll 1955	0–200	85		
Pacific Oceanic Fisheries Investigations, Cruise 5 1950 (POFI)	0–200	51		
POFI Cruise 8 1951	0–200	87		
Pelagic Area Studies 1954	0–25,25–50,50–75,75–100, 100–300,300–500,500–700	138		50
U. S. S. Nereus 1947	0–100,0–200			28
U. S. S. Burton Isl. 1950 (Chukchi and Beaufort Seas)	0–100			53
U. S. S. Burton Isl. 1951 (Bering Sea)	0–50			10
U. S. S. Burton Isl. 1951 (Beaufort Sea)	0–100			56
U. S. S. Burton Isl. 1953 (Pr. Wales Str.)	0–100			30
U. S. C. G. C. North Wind 1954 (Banks Isl.)	0–50			21
Chinook 1956	0–100	9		
Equapac 1956	0–300	40		
Marine Life Res. 1939 (MLR)	0–60,60–120	32		
MLR 1941	0–100	108		
MLR 1949–1954	0–70,0–140	1059		
MLR 1950 (deep)	0–600,0–1000	65		
Miscellaneous 1933–1951		95		168
Total.....		2425	67	454

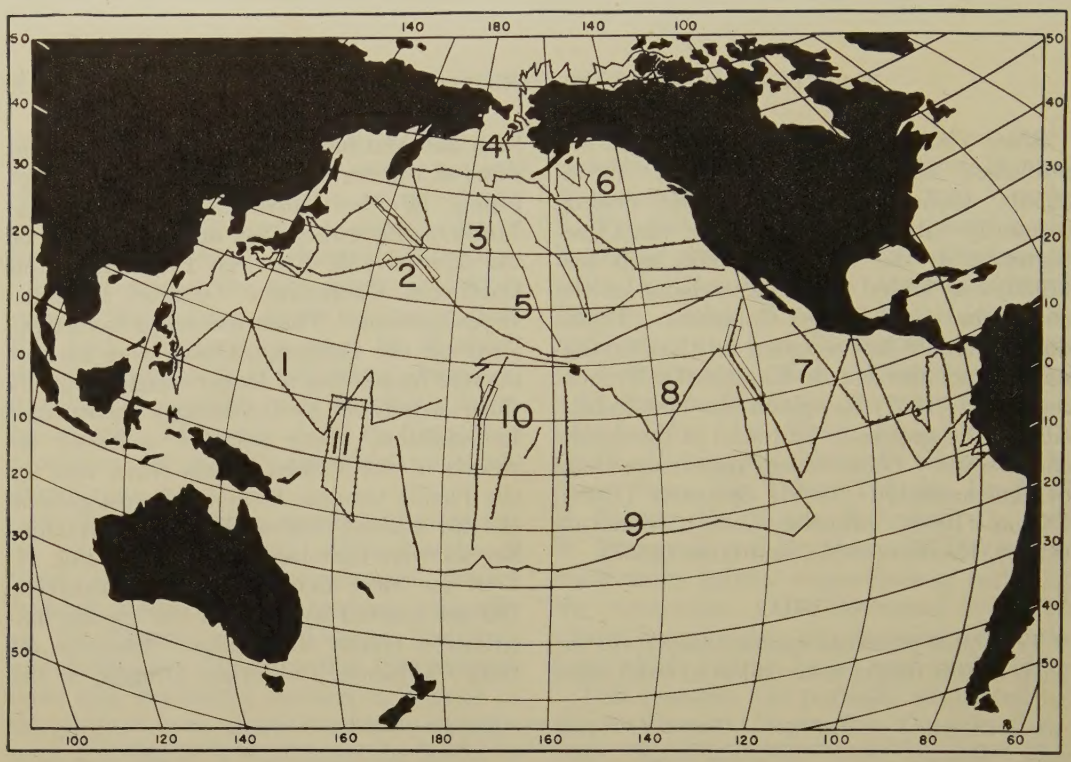

FIG. 1. Generalized tracks of the major expeditions reported in this paper. (1) Troll, (2) Transpacific, (3) Chinook, (4) U. S. S. Burton Island, (5) U. S. S. Nereus, (6) Northern Holiday, (7) Shellback, (8) Midpacific, (9) Capricorn, (10) Pacific Oceanic Fisheries Investigations, (11) Equapac. Locations of temperature, salinity, and oxygen sections shown in Figures 24–26, from Transpacific Expedition and Station No. 112, are indicated by blocked areas.

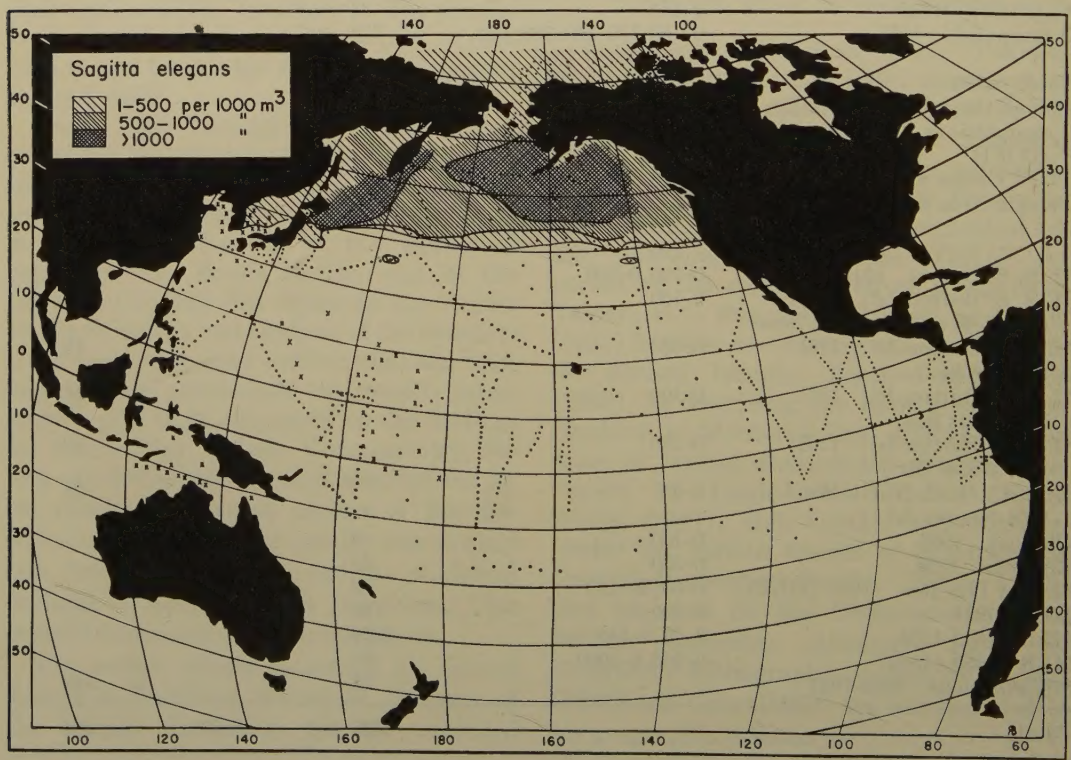

FIG. 2. Distribution of *Sagitta elegans* in the Pacific and regions to the north. ×'s are stations reported by Tokioka 1940a, 1940b, 1942, 1951, 1955a, and 1956. The species was found only in the shaded area.

Gulf of California, and some of the stations off Peru, Japan, and the Philippines are not located on the charts because of the close spacing of the stations in those areas. For the same reason only 40 of about 150 stations in the Arctic between 110° and 165° W. Long. are charted. The intensity of sampling at the stations varied from 1 to 18 net tows per station at any one time, and many stations were occupied two or more times.

Station locations, dates, times, and depth of tows for the Pacific Oceanic Fisheries Investigations are given in King and Demond (1953), for the Marine Life Research cruises in Staff, South Pacific Fisheries Investigations (1954), for Long Line Expedition in Wooster and Jennings (1955), and for the U.S.S. Burton Island Expeditions in Johnson (1956). Mimeographed lists of the station locations, dates, times and depths of tows for Transpacific, Pelagic Area Studies, Shellback, Northern Holiday, Chinook, Troll, Capricorn, and Mid-Pacific Expeditions are available in the Division of Marine Invertebrates, Scripps Institution of Oceanography. A summary of the original data on which this paper is based is deposited in the Library of the Scripps Institution. Identified specimens of most of the species discussed have been deposited in the Division of Marine Invertebrates of Scripps Institution and in the United States National Museum (U.S.N.M. catalog numbers 28688 through 28705).

FIELD OPERATIONS

Several types of nets were used to collect the samples, at various depths and in different ways (Table 1). Most of the one-meter nets were equipped with current meters and usually filtered about 1,000 cubic meters of water per tow. The one-meter nets had a mesh of 0.65 mm (#30 xxx silk grit gauze). The one-half meter nets were of varying mesh sizes of which the most common was 0.2 mm. The great majority of net tows were oblique from the stated depths to the surface. However, on Transpacific Expedition and Pelagic Area Studies, opening-closing nets were used in oblique tows so that the water column was divided into the indicated depth intervals. The construction and use of the one-meter nets are described in greater detail by the Staff, South Pacific Fishery Investigations (1952, 1953, 1954, 1955) and by King and Demond (1953). In the Arctic regions, because of the difficulty of maneuvering in ice, all tows were vertical, frequently from the sea bottom to the surface. All samples were preserved in dilute formalin.

LABORATORY PROCEDURES

In the early phases of analysis the chaetognaths were removed from the sample or from an aliquot of the sample and examined microscopically. This traditional approach to zooplankton analysis was soon abandoned, not only because it was too time-consuming, but also because many species that are sparsely distributed were not adequately represented in the aliquots. Instead of sorting, each sample was poured into a large tray 50 cm long by 20 cm wide, marked into 1,000 one-centimeter squares and examined with a binocular microscope, using transmitted light and 12 × magnification. The abundance of the various species was tabulated on hand counters or tallies until a total of 100 or more specimens of all species had been examined. For each species the percentage of the sample examined microscopically was determined by recording the number of centimeter squares examined to find the number of specimens that were counted (up to 30, occasionally more). The total number of each species in the sample was then computed on this basis. The percentage of the sample examined for each species varied from 0.1 to 100, but for most species was usually about ten per cent. After microscopic examination by the one-centimeter squares, the remainder of each sample was carefully scanned with the unaided eye to check for other recognizable species. Poorly preserved, damaged, and very small specimens were removed and examined at higher magnifications.

In the one-meter net samples nearly all specimens could be identified as to species except for badly mangled specimens and immature individuals of the *serratodentata* group. Specimens too small to be positively identified were recorded as juvenile chaetognaths.

The number of specimens of each species

in 1,000 cubic meters of water was then calculated from the amount of water filtered by the net, the percentage of the sample examined for the species, and the number of specimens found. Duplicate counts of several samples indicate that the variation between net samples due to patchiness is considerably greater than variations in the counting procedure. In order to achieve some standard method in charting species abundance, the following procedures were followed. First the total range was outlined. The limits of each species were drawn so that in general the smallest possible area of occurrence was shown. The contour intervals were made as large as possible in order to reduce the effects of patchiness and at the same time provide three or four concentration ranges. As far as possible, the same contour intervals were used for species with the same general abundance. All absences are shown on the charts.

VERTICAL DISTRIBUTION

One of the most intensive and pioneering works on the vertical distribution of zooplankton was carried out by E. L. Michael (1911) on the Chaetognatha in the San Diego region. Thomson (1947) described the vertical distribution of the chaetognaths off eastern Australia. Although data on the vertical distribution of the chaetognaths in the present material are avaialable from Transpacific Expedition, Pelagic Area Studies, and some collections in the Marine Life Research cruises, these data have not yet been studied in detail. In general, however, they confirm the work of Michael and Thomson. The only notable exceptions are found in the equatorial region, where certain mesoplanktonic and bathypelagic species are found at shallower depths than to the north and south.

All species discussed in this paper, unless otherwise stated, have their maximum abundance in the upper 100 meters of water and their lower limits at 300 to 400 meters. Because most of the net tows were from the surface to 200 to 300 meters, in the following charts of species distributions the concentrations are thought to represent the average concentration of the species in the upper 200 to 300 meters of water.

DISTRIBUTION PATTERNS IN RELATION TO THE WATER MASSES

Sagitta elegans Verrill

(Fig. 2)

The distribution of *Sagitta elegans* in the Pacific and areas to the north marks it as a northern, cold-water species. In general this species appears to be most abundant near shore. In the Arctic it decreases in concentration as the pack ice is penetrated. A section (Fig. 3) from shore into deep water, taken off Point Barrow, Alaska, in 1950 by the U.S.S. Burton Island illustrates the decrease in abundance with penetration of the pack ice. The report of Bogorov (1946) indicates that it is absent from the central region of the Arctic basin; however, his sampling was not intensive enough to prove this.

The southern boundary of *Sagitta elegans* at about 40° to 41° N. Lat. appears to agree very well with the southern limit of the Pacific Subarctic Water (Figs. 4 and 5) as shown by Sverdrup, Johnson, and Fleming (1942). The occurrence of *S. elegans* at Transpacific Station 112 (36° 35′ N. Lat., 163° 46′ E. Long.), considerably south of its usual southern limit, is accompanied by an absence of many warm-water species such as *Sagitta bedoti*, *S. pseudoserratodentata*, *S. californica*, *S. regularis*, and *S. pacifica* (Figs. 18, 12, 10, 14, and 9). Two net tows were taken at this station. The upper tow from 0 to 200 meters had no *S. elegans* but contained *S. enflata*, *Pterosagitta draco*, and *Sagitta hexaptera* (Figs. 6, 7, and 8). The presence of these widespread, warm-water species would indicate some diluted Central Water present in the upper 200 meters. The lower net tow (200–400 meters) contained *Sagitta elegans* but no species that can be considered a warm-water inhabitant. Several mesoplanktonic species such as *Sagitta* sp. (*serratodentata* group), *S. minima*, *Krohnitta subtilis*, and *Sagitta decipiens* were also present in the deeper net tow. The fauna at this station is interpreted as an isolated community that was carried considerably south of its usual range. The same phenomenon is shown at Transpacific Station 60 (44° 46′ N. Lat., 159° 55′ E. Long.), where a segment of the warm-water

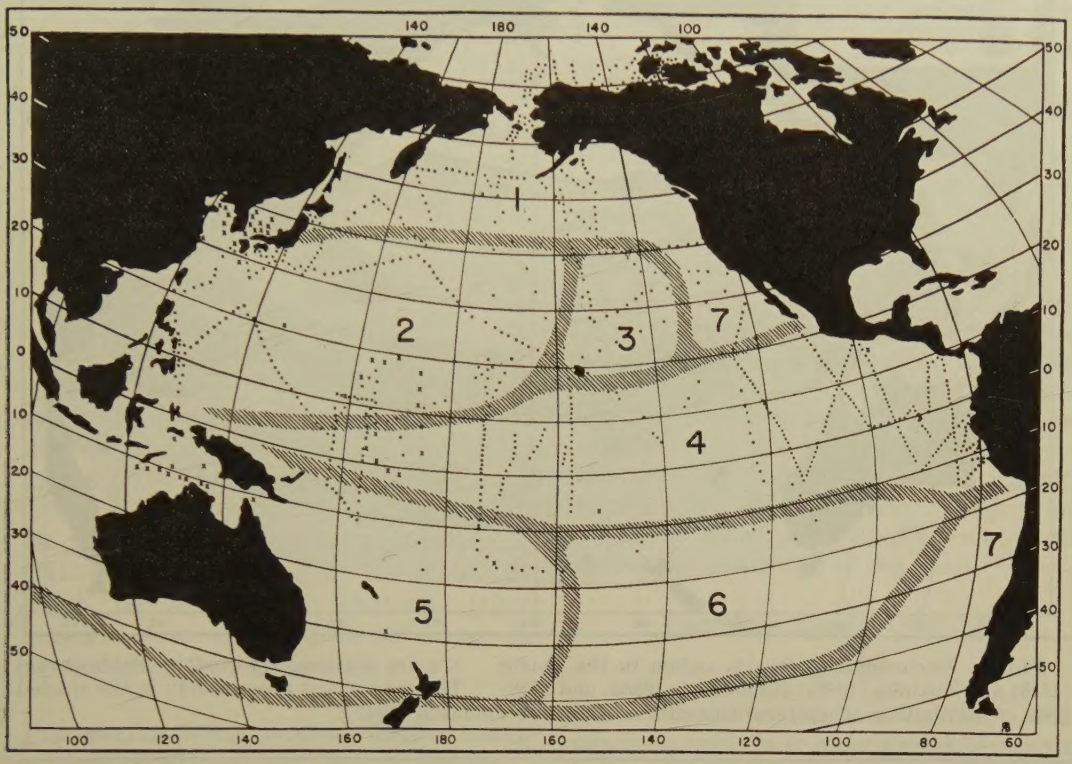

FIG. 4. Water masses of the Pacific (100–500 meters) according to Sverdrup, Johnson, and Fleming (1942). (1) Pacific Subarctic Water, (2) Western North Pacific Central Water, (3) Eastern North Pacific Central Water, (4) Pacific Equatorial Water, (5) Western South Pacific Central Water, (6) Eastern South Pacific Central Water, (7) Transition Water.

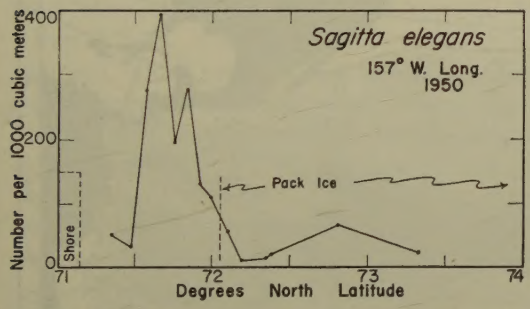

FIG. 3. Concentration of *Sagitta elegans* in the upper 100 meters of water in a section due north from Point Barrow, Alaska. Note the rapid decrease in abundance with penetration of the pack ice.

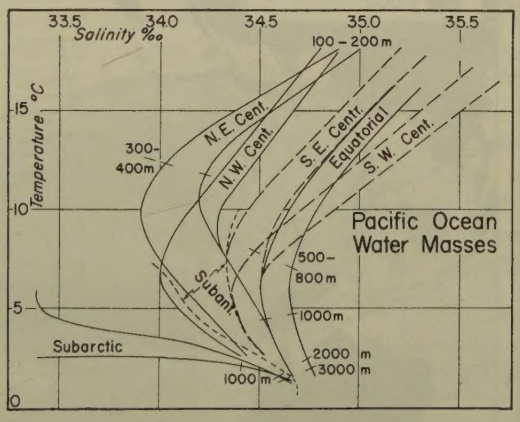

FIG. 5. Temperature-salinity relationships of the Pacific water masses below 100 meters, based on Sverdrup, Johnson, and Fleming (1942).

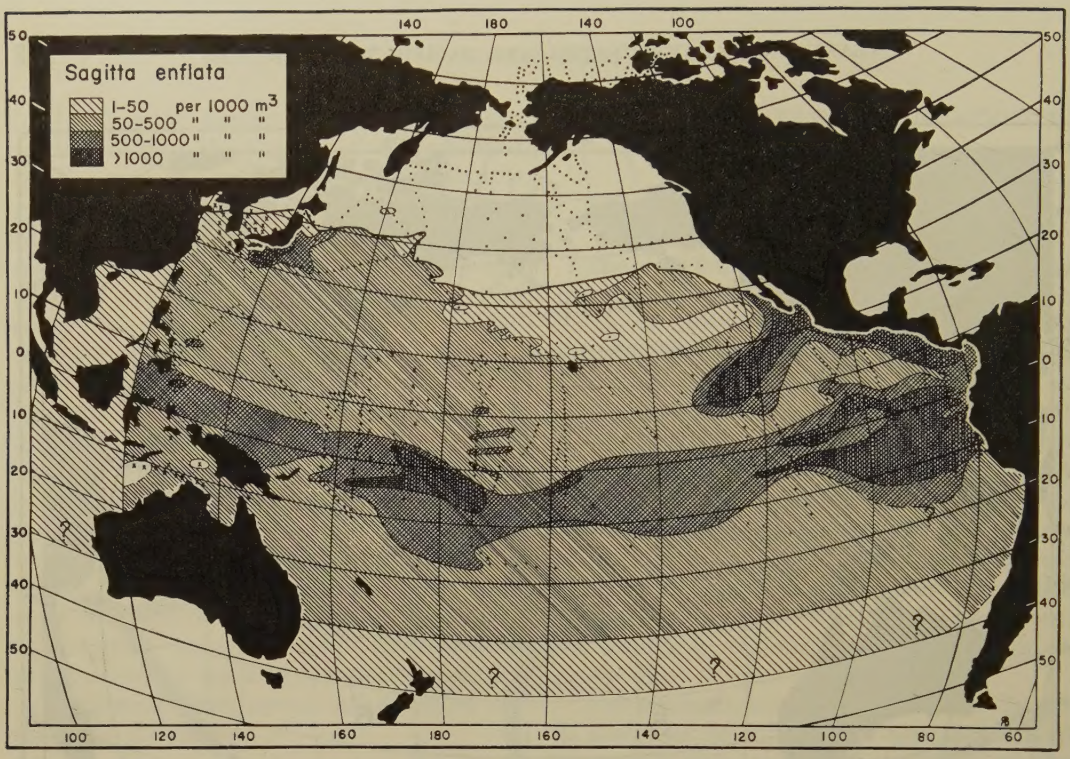

FIG. 6. Occurrence of *Sagitta enflata* in the Pacific. ×'s are stations reported by Baldasseroni (1915) and Tokioka (1940a, 1940b, 1951, 1955a, and 1956). The species was present only in the shaded area. Distribution off eastern Australia is based on Thomson (1947).

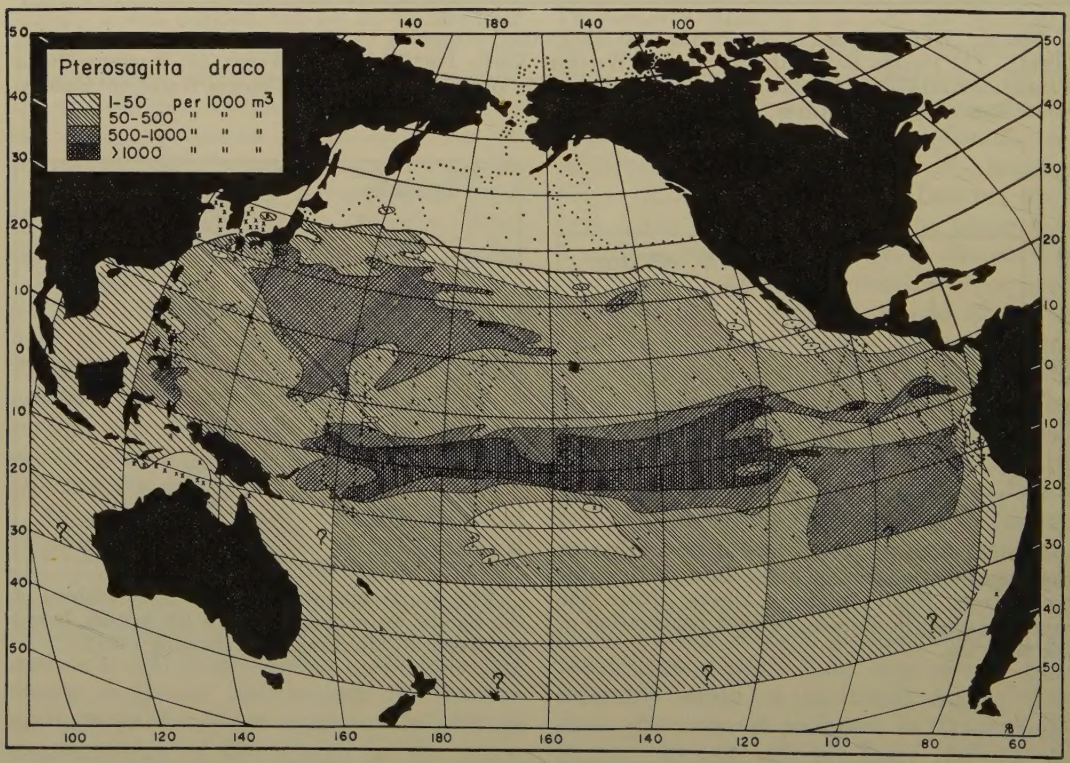

FIG. 7. Occurrence of *Pterosagitta draco* in the Pacific. ×'s as in Figure 6. Distribution off eastern Australia is based on Thomson (1947).

fauna has been carried north of its usual range (see *S. enflata*, *Pterosagitta draco*, *Sagitta bedoti*, *S. minima*, Figs. 6, 7, 18, and 21). This expatriated community has become impoverished in number of species of chaetognaths due to some mixing with Subarctic Water (*S. elegans* was present).

Sagitta enflata Grassi

(Fig. 6)

The northern limit of another well-known chaetognath, *Sagitta enflata*, at about 40° N. Lat., approximates the southern limit of *S. elegans*. The southern limit of *S. enflata* in the Pacific has not been definitely established, but is probably in the region of 40° S. Lat. at the subtropical convergence. Baldasseroni (1915) recorded it at 35° south off Chile, and Thomson (1947) reported it as far south as 38° along the southeastern Australian coast.

Pterosagitta draco (Krohn), **Sagitta hexaptera** d'Orbigny, and **Sagitta pacifica** Tokioka (**serratodentata** group)

(Figs. 7–9)

The distributions of these three species are essentially similar to that of *Sagitta enflata*. The four occupy the Equatorial and Central Water Masses of the Pacific (Figs. 4–5). This type of distribution pattern, which can be called a cosmopolitan warm-water or widespread warm-water distribution, is very common among planktonic organisms and led Giesbrecht (1892), working on copepods, and many other workers including Ekman, in his review of marine zoogeography (1953), to divide the pelagic realm into three faunas—a warm-water fauna, and northern and southern cold-water faunas. There can be no doubt that such a division exists; however, as will be shown later, it is convenient to speak of smaller pelagic divisions as faunas rather than subfaunas, and here these three major divisions will be spoken of as provinces.

Sagitta californica Michael[3]

(Fig. 10)

The distribution of *Sagitta californica*, called *S. bipunctata* by most recent authors, is considered a special type of widespread, warm-water distribution which may be called anti-equatorial. Hubbs (1952) has suggested the term antitropical for species that avoid the tropics, including, as a special case, those that were formerly called bipolar. "Anti-equatorial" may be applied as another type of antitropicality, to the distribution of such species as *S. californica*, which reach to within five or ten degrees of the equator. The species is absent from more than 95 per cent of the stations occupied in a narrow band in the equatorial region, but occurs at more than 95 per cent of the stations on either side of this band.

Eukrohnia hamata (Möbius)

(Fig. 11)

Several species that are associated with relatively cold water show a marked increase in concentration in the band where *Sagitta californica* is extremely rare. In the San Diego region and along the coast of Baja California *Eukrohnia hamata* occurs only below 500 meters. Yet in the equatorial region shown in Figure 11 it occurs commonly above 300 meters. *E. hamata*, which is found in the upper 100 meters of the Arctic and Antarctic, shows the classic tropical submergence, but it also shows an equatorial emergence. Other examples of relatively cold water species that are more abundant in this equatorial band are *Sagitta decipiens*, *S. minima* (Fig. 21), *S. planctonis*, and *Eukrohnia fowleri*.

[3] Although many recent authors have followed Ritter-Zahony (1911a) and used the name *Sagitta bipunctata* for an oceanic, warm-water species, this species is here called *S. californica*. The name *S. bipunctata* has been used for many species of Chaetognatha, while *S. californica*, which was very thoroughly described by Michael (1913), has been used exclusively for this oceanic species. Until the status of the name *Sagitta bipunctata* is definitely settled, it seems best to use the more precise name, *Sagitta californica*.

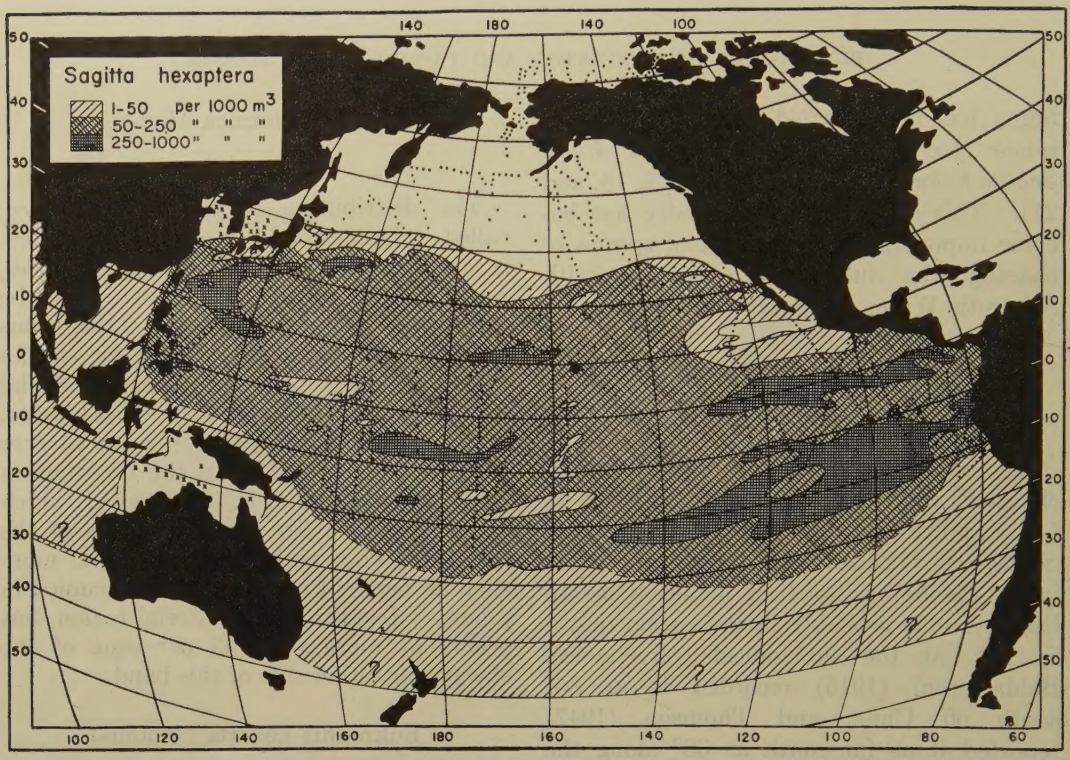

FIG. 8. Distribution of *Sagitta hexaptera* in the Pacific. ×'s as in Figure 6. Distribution off eastern Australia is based on Thomson (1947).

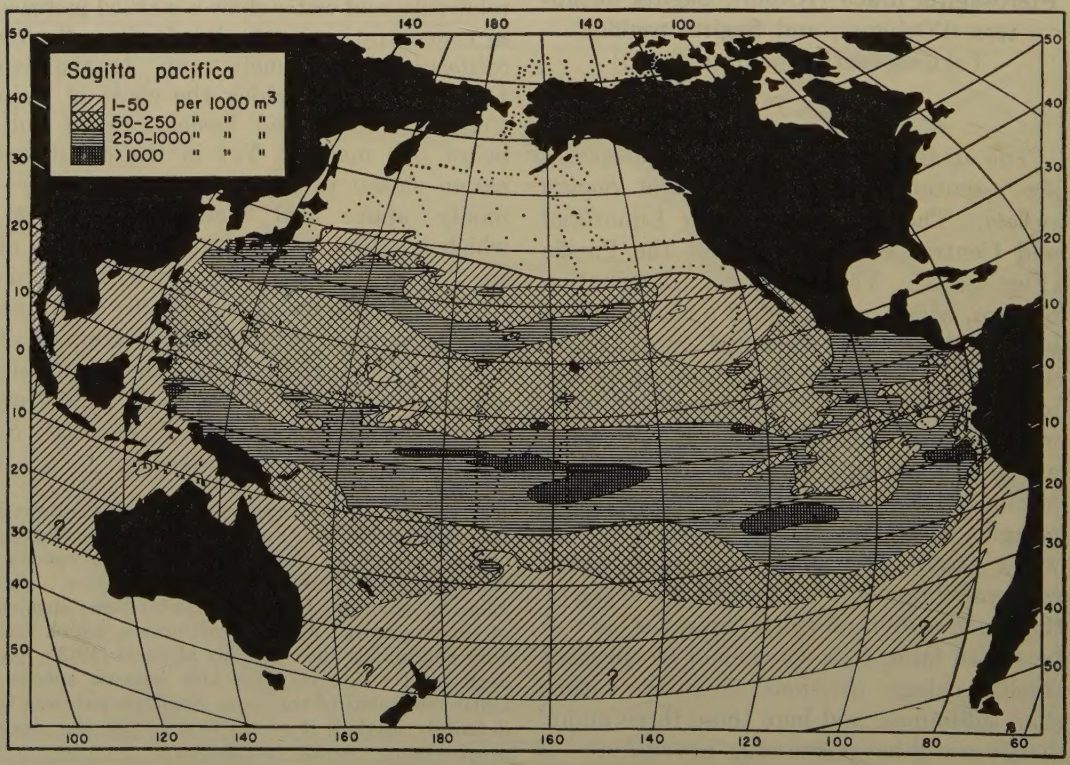

FIG. 9. Occurrence of *Sagitta pacifica* (*serratodentata* group) in the Pacific. ×'s are from Tokioka (1940b and 1956). Distribution off eastern Australia is based on Thomson (1947).

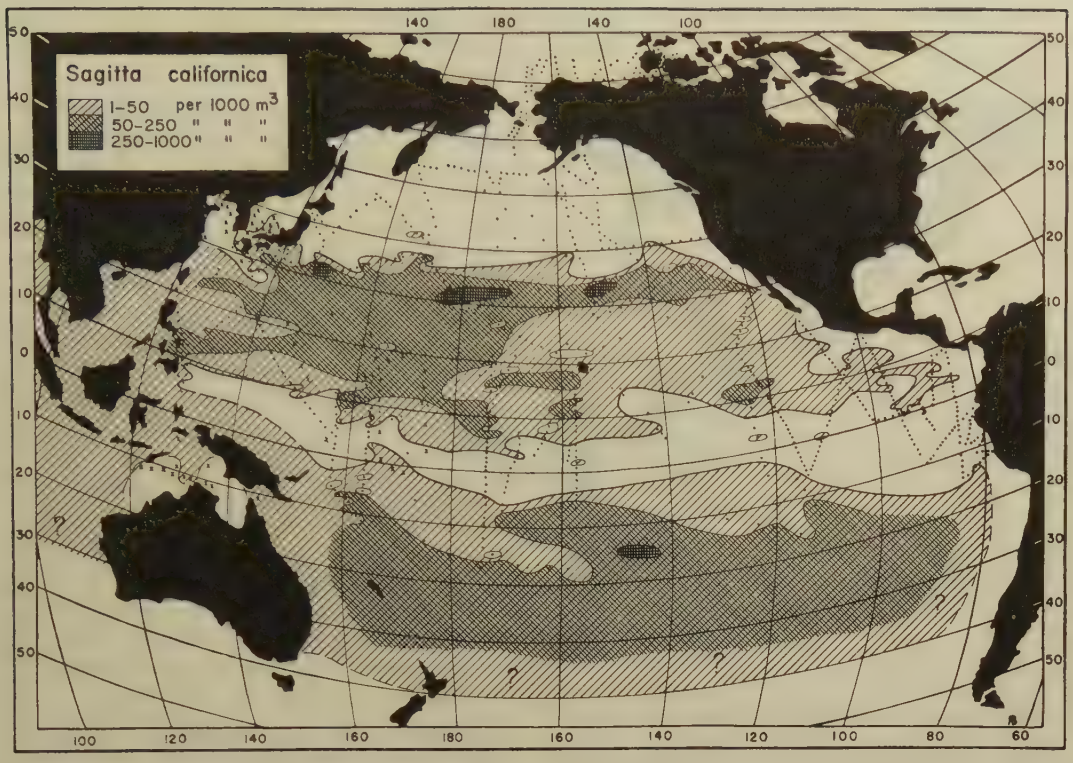

FIG. 10. Distribution of *Sagitta californica* in the Pacific. ×'s as in Figure 2. Distribution off eastern Australia is based on Thomson (1947).

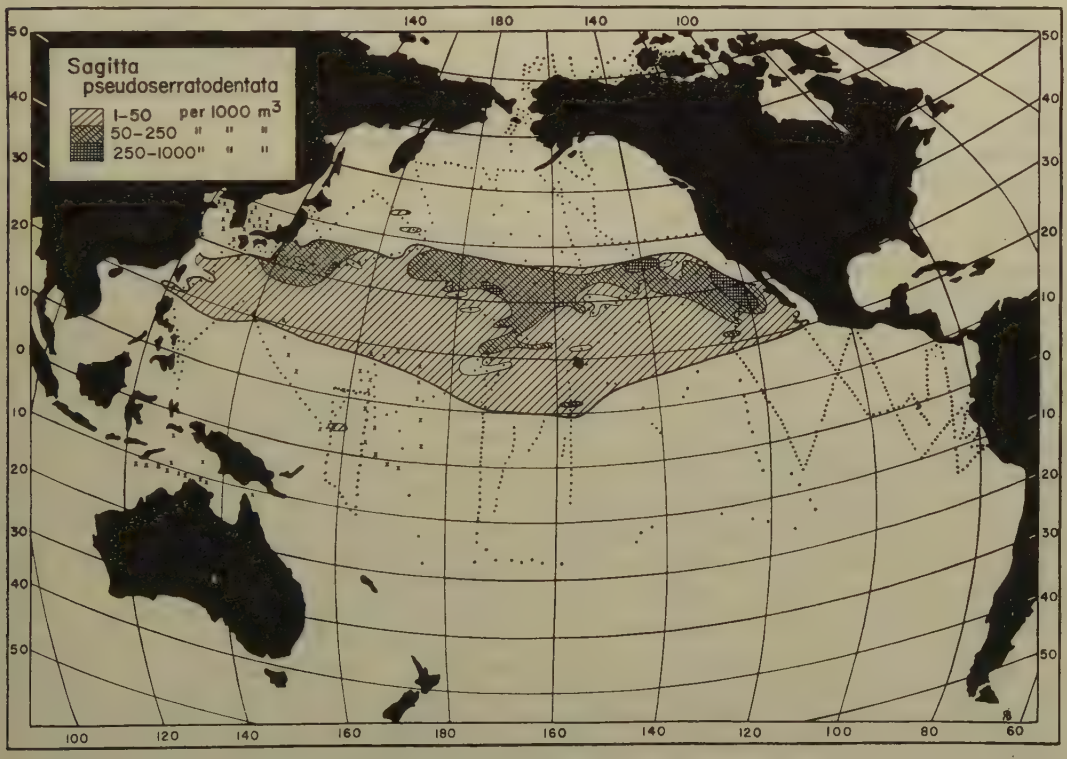

FIG. 12. Distribution of *Sagitta pseudoserratodentata* in the Pacific. The limits of this species approximate fairly closely the limits of the Pacific Central Water (Fig. 4). ×'s as in Figure 2.

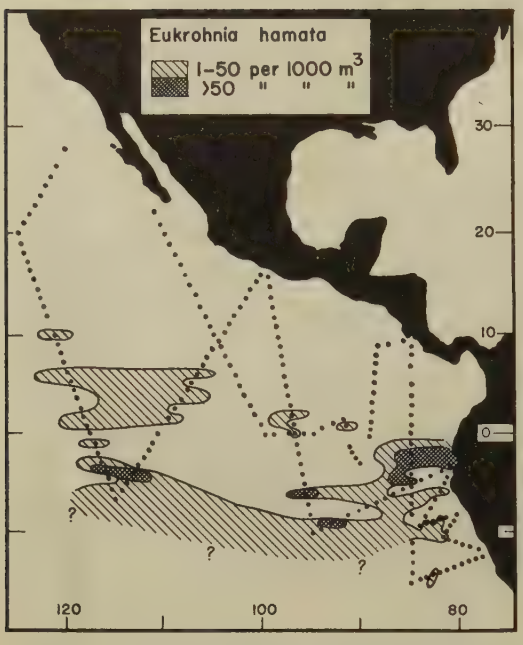

FIG. 11. Concentration of *Eukrohnia hamata* in the upper 300 meters of water in the eastern equatorial Pacific.

Sagitta pseudoserratodentata Tokioka[4]

(Fig. 12)

The Equatorial Water Mass forms a barrier that almost completely isolates the northern and southern populations of *Sagitta californica*. This Water Mass is apparently an even more formidable barrier to the southern penetration of *Sagitta pseudoserratodentata*. It is evident that the limits of this species need more extensive and intensive sampling, particularly along its southern boundary between 130° and 150° W. Long. and 140° to 160° E. Long. The boundaries are most reliably established off California and south of Hawaii, where some seasonal sampling has been carried out. The Pacific Oceanic Fisheries Investigations samples of June–August 1950, and January–March 1951, indicate a surprisingly stable boundary at 10° N. Lat., between 158° and 172° W. Long. In four crossings, the southern limit was at 10° N. Lat. three times and at 9° once. To the west of this region between 150° and 170° E. Long., the boundary is still poorly defined. Tokioka (1942, 1954b, 1955a) in discussing the chaetognaths from this western region, reported *Sagitta pseudoserratodentata* from one station (5° 3′ N. Lat., 155° 53′ E. Long.) far to the south of what appears to be its southern limit. This species roughly occupies the Central Water Masses of the North Pacific (Fig. 4), with the poorest fit in the southwest part of the Western North Pacific Central Water. It penetrates to the coast of Baja California as do the cosmopolitan warm-water species. From the standpoint of the species present, this water is more characteristic of the East Pacific Central Water than of the California Current or Transition Water as described by Sverdrup, Johnson, and Fleming (1942).

Tokioka (1954a) also reported *Sagitta pseudoserratodentata* close to the east coast of Japan. In the Transpacific and Troll Expeditions it was not found there (Fig. 12). According to Tokioka, who has carried out seasonal sampling, the distribution of the chaetognaths along the coast of Japan changes considerably with time. Over a period of 12 months he found that *S. pseudoserratodentata* formed only 1.3 per cent of the chaetognath fauna in Sagami Bay, indicating that only a very small amount of Central Water penetrates the Bay during the year. In a dense swarm of chaetognaths associated with a small red tide in the Bay, *S. pseudoserratodentata* formed only two per cent of the chaetognath fauna. Off the Southern California coast on the other hand, in the Pacific Central Water, *S. pseudoserratodentata* often makes up 20 per cent of the chaetognath fauna. It would seem that this species might be found in the South Pacific Central Water, but so far it has not been taken there. Because the distribution of this species corresponds rather closely to that of the North Pacific Central Water (Fig. 4), it is best described, zoogeographically, as a "central species"; and it is thought that *Sagitta pseudoserratodentata* is representative of a large group of species of other animal phyla

[4] A revision of the *serratodentata* group has been proposed by Furnestin (1953, 1957). Her nomenclature is partially followed, but *Sagitta pseudoserratodentata* is regarded here as a valid species (Bieri 1957).

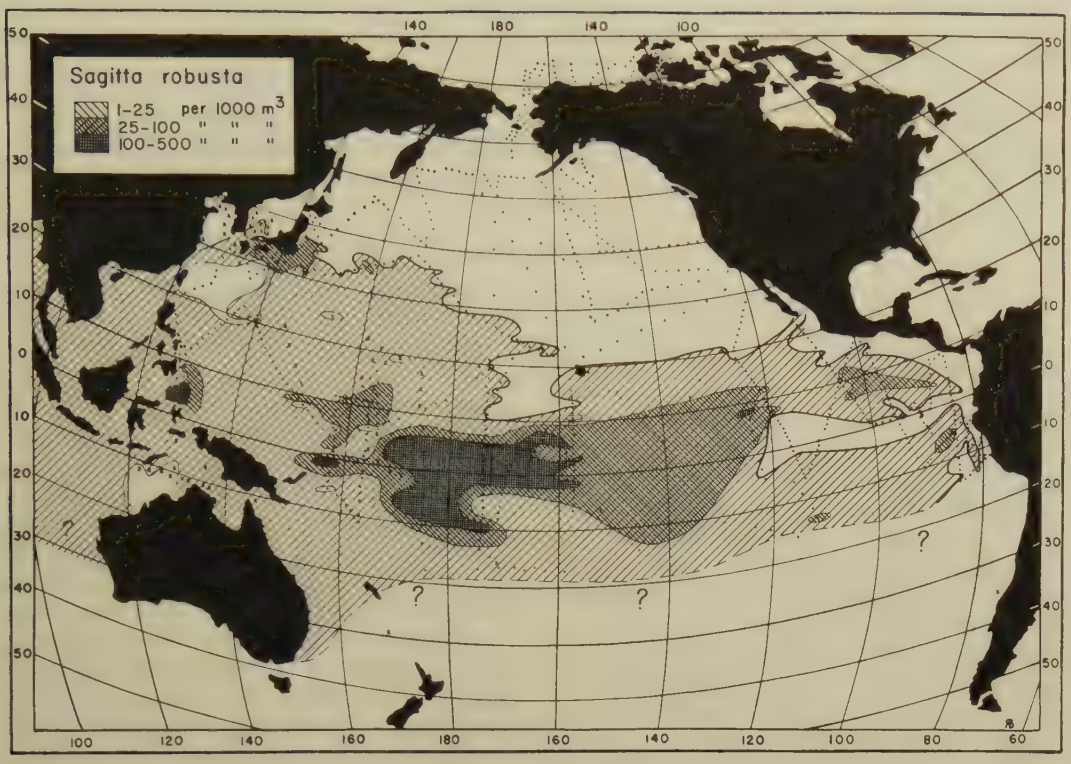

FIG. 13. Occurrence of *Sagitta robusta* in the Pacific. This species is absent from the Eastern North Pacific Central Water. ×'s as in Figure 6. Distribution off eastern Australia is based on Thomson (1947).

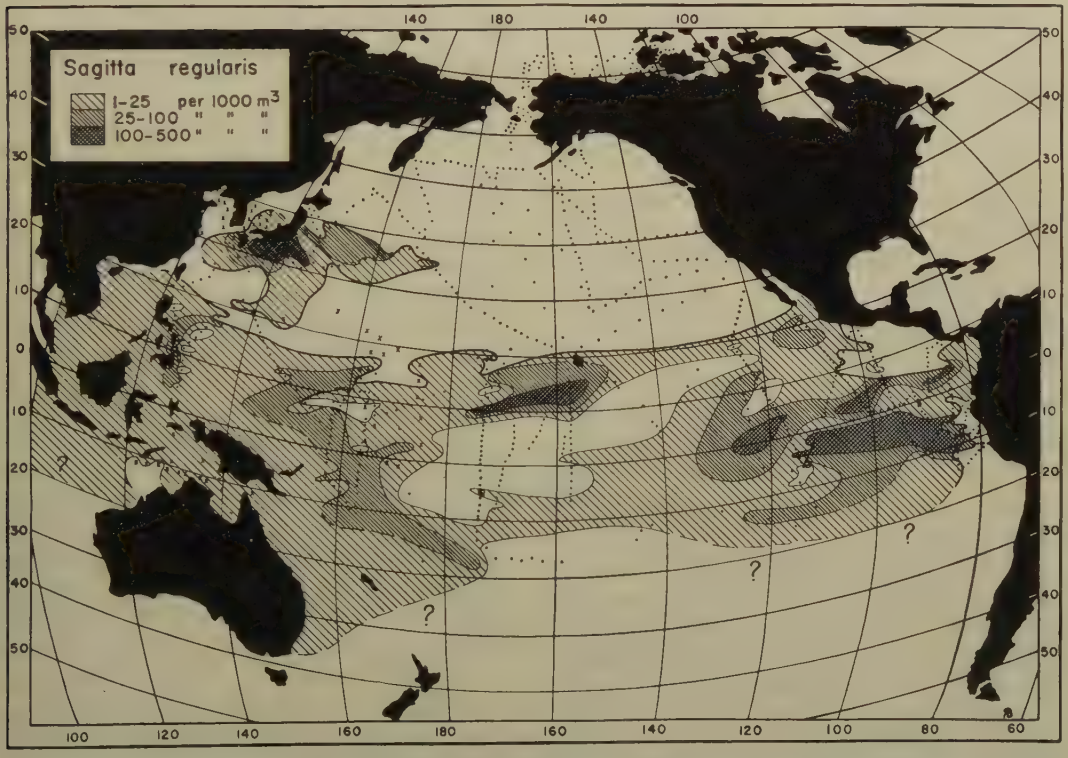

FIG. 14. Distribution of *Sagitta regularis* in the Pacific. The distribution of this species is similar to that of *Sagitta robusta*. ×'s as in Figure 2. Distribution off eastern Australia is based on Thomson (1947).

that comprise a distinctive North Pacific Central Fauna.

Sagitta robusta Doncaster

(Fig. 13)

The distribution of *Sagitta robusta* appears to be typical of a number of species of Chaetognatha. It occurs throughout most of the equatorial region and spreads into the Central Water Masses in the Western Pacific. It is absent from the Eastern North Pacific Central Water Mass. Whether or not it is absent from the Eastern South Pacific Central Water has not been established. Since this water mass is very similar to the Pacific Equatorial Water in its temperature and salinity relationships, the species might be able to penetrate this area (Figs. 4–5). In its absence from the region of the Galapagos, *S. robusta* recalls *S. californica* (Fig. 10).

Although this type of distribution can be described as tropical, it seems best to use the term equatorial-west-central, because the species occurs far to the north and south of the tropical zone in the Western Pacific.

Sagitta regularis Aida, **Krohnitta pacifica** (Aida), and **Sagitta ferox** Doncaster

(Figs. 14–16)

These species are regarded as essentially equatorial-west-central species with the extremes of their ranges similar to that of *Sagitta robusta*. However, they are more patchy in their distribution and present a rather confused picture.

Sagitta regularis, like *S. robusta*, is absent from the Eastern North Pacific Central Water (Fig. 14). Much of the area in the center of its range where it has not yet been found may be filled in by future expeditions using larger nets.

Krohnitta pacifica is absent in a band from about 5° to 15° N. Lat. almost across the Pacific (Fig. 15). Both it and *Sagitta ferox* (Fig. 16) extend slightly into the Eastern North Pacific Central Water, northeast of Hawaii, whereas *S. robusta* and *S. regularis* do not.

Sagitta friderici Ritter-Zahony, **Sagitta crassa** Tokioka, **Sagitta bedoti** Beraneck, **Sagitta neglecta** Aida, and **Sagitta pulchra** Doncaster

(Figs. 17–20)

The distributions of the preceding eleven species show varying degrees of association with the water masses. There are other species that apparently cut across water masses or have limits which do not correspond with the water masses. These species can be divided into three major groups. First there is a group of species that live primarily in the upper 200 meters, which because they are most abundant near shore can be characterized as neritic or nearshore, although they may actually extend hundreds of miles out to sea. *Sagitta friderici*, *Sagitta crassa*, *S. bedoti*, *S. neglecta*, and *S. pulchra* are examples. Because it is very abundant near shore, *S. elegans* could be placed in this group, even though it appears to extend across the Pacific at 40° N. Lat.

The dependence of various species of Chaetognatha on "nearshore water" has been noted by several authors. Several explanations for this phenomenon have been advanced, each with some points in its favor. These arguments are too lengthy to be presented here in detail. It can be said, however, that there are four chief explanations: (1) unknown dissolved substance in the water, (2) static temperature-salinity relationships, (3) dynamic temperature-salinity relationships, and (4) biologic restriction through competition. The distribution of *Sagitta friderici* off California, Peru and Chile, and North and South Africa, is correlated with upwelling and suggests that temperature and salinity are related to the distribution pattern of this species. Michael (1911) has shown that off California this species, which he called *S. bipunctata*[5], migrates toward the surface at night and is most abundant during the day at about 60 meters. This is the average depth of the thermocline in that region. Although *S. friderici* may be able to stay above the thermocline, the fact that it is

[5] Based on an examination by the author of 280 vials containing chaetognaths identified by E. L. Michael.

FIG. 15. Occurrence of *Krohnitta pacifica* in the Pacific. Note that it extends slightly into the Eastern North Pacific Central Water northeast of Hawaii. ×'s as in Figure 2. Distribution off eastern Australia is based on Thomson (1947).

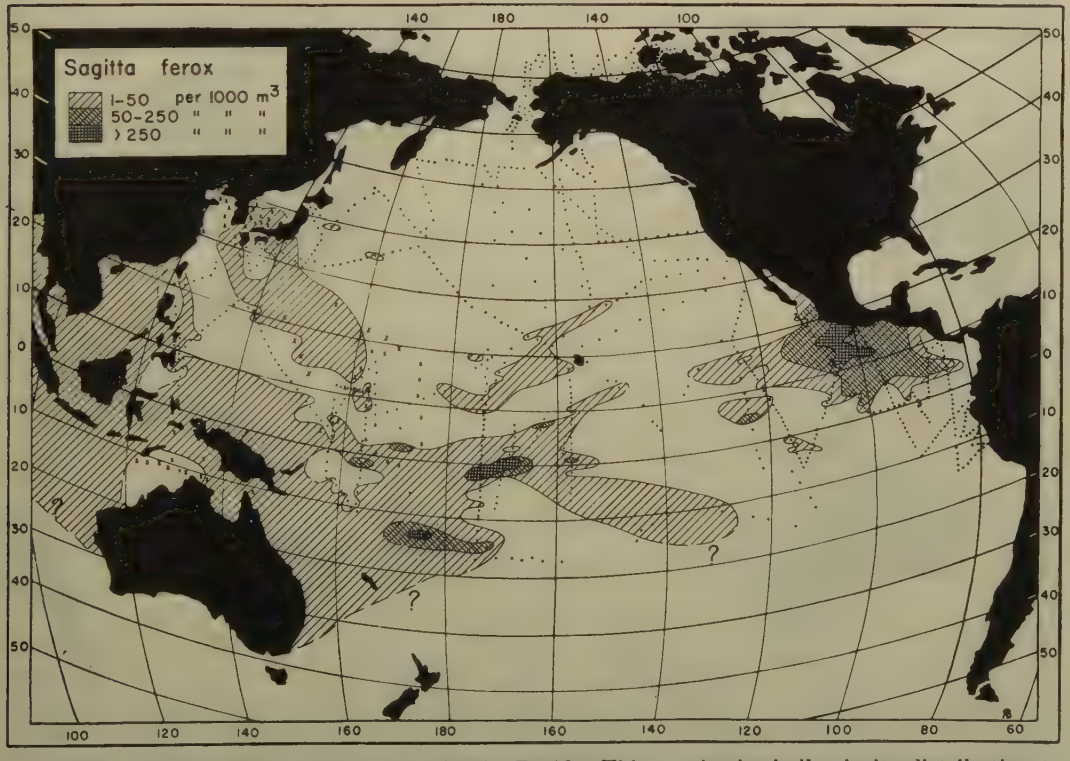

FIG. 16. Distribution of *Sagitta ferox* in the Pacific. This species is similar in its distribution to *Krohnitta pacifica*. ×'s as in Figure 2. Distribution off eastern Australia is based on Thomson (1947).

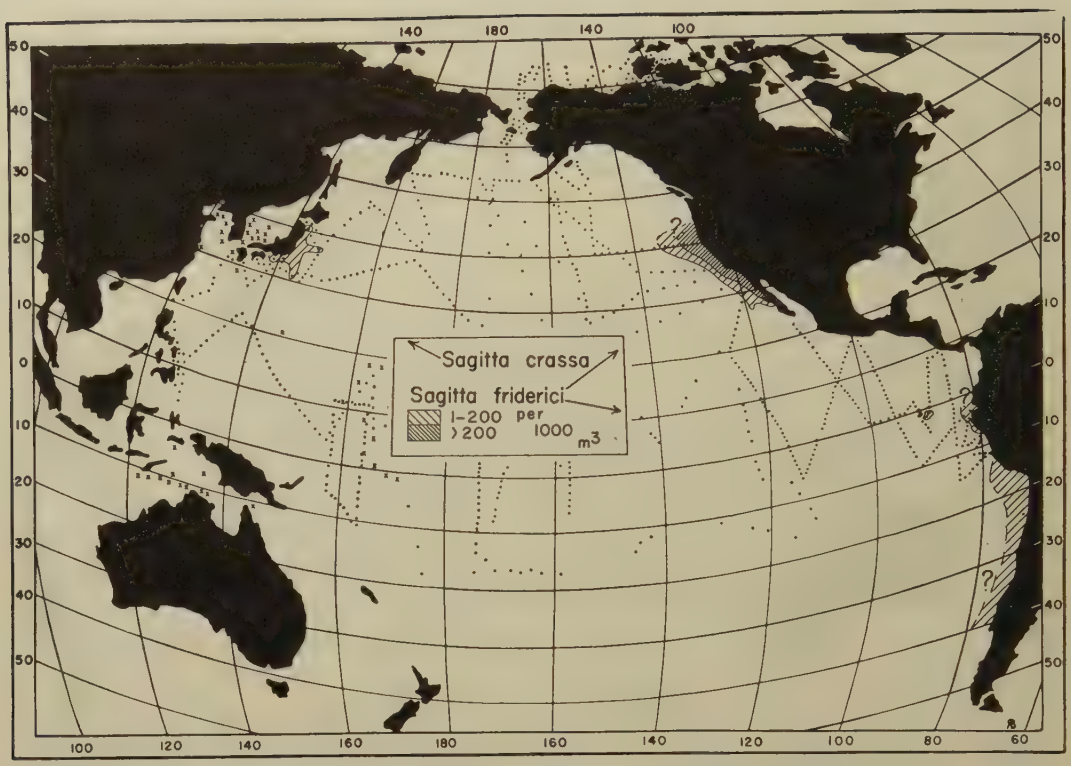

FIG. 17. Known extent of the two *Sagitta friderici* populations in the Pacific. This species dominates the California and Peru Currents. *Sagitta crassa* off Japan is a closely related species. ×'s as in Figure 2.

FIG. 18. Known extent of the two *Sagitta bedoti* populations in the Pacific. The distribution of this species is reminiscent of the equatorial-west-central species such as *Sagitta robusta*, but it is apparently unable to cross the oceanic equatorial region. ×'s as in Figure 2. Distribution off eastern Australia is based on Thomson (1947).

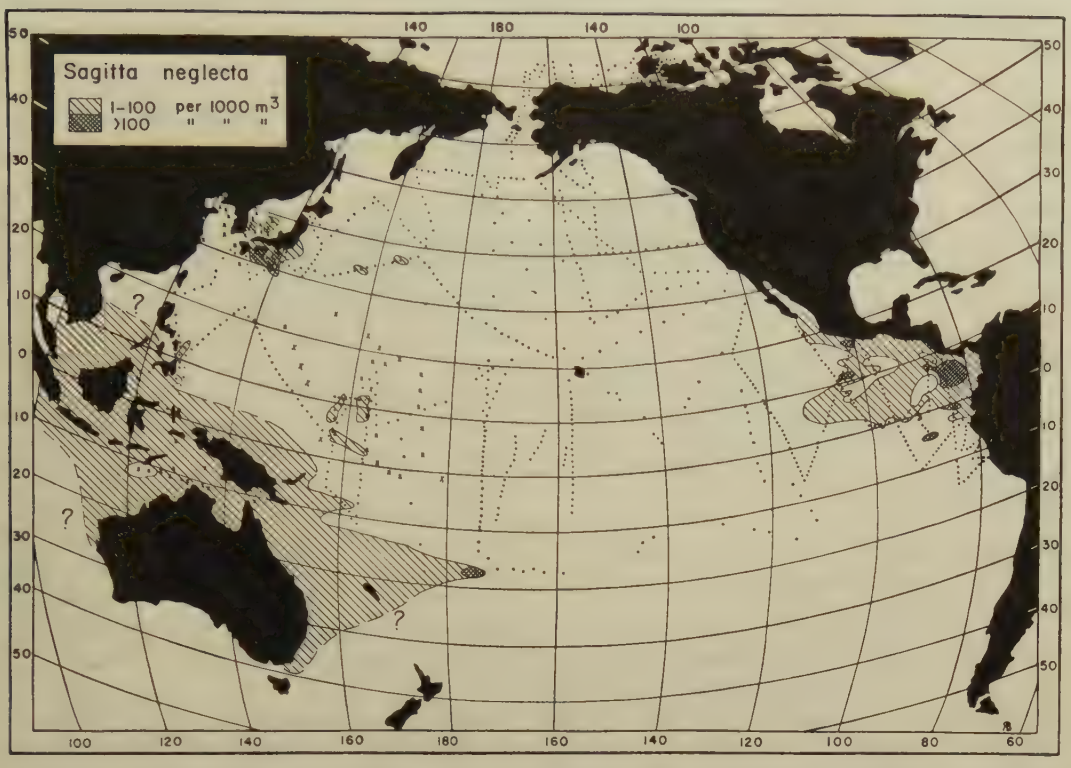

FIG. 19. Known extent of *Sagitta neglecta* in the Pacific. It has essentially the same distribution as *Sagitta bedoti*, but is not so abundant as that species. ×'s as in Figure 2. Distribution off eastern Australia is based on Thomson (1947).

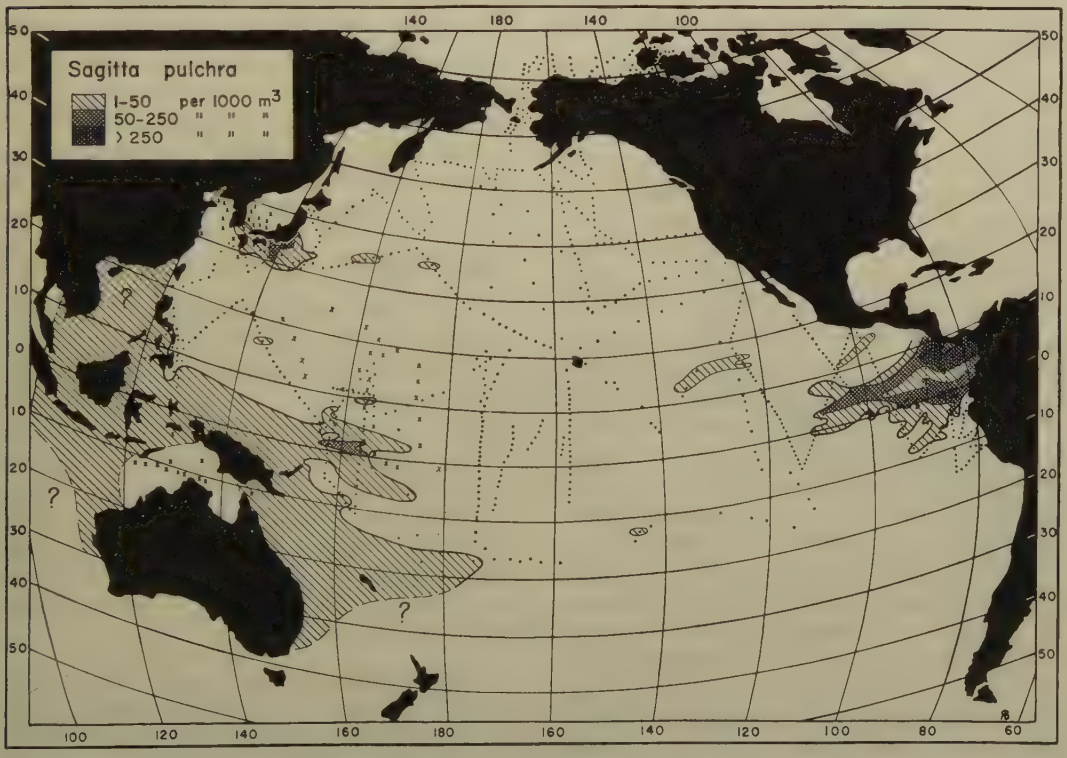

FIG. 20. Known extent of *Sagitta pulchra* in the Pacific. It is similar in its distribution to *Sagitta bedoti* and *S. neglecta*. ×'s as in Figure 2. Distribution off eastern Australia is based on Thomson (1947).

often taken at depths down to 200 meters indicates that it is able to withstand rapid and pronounced temperature changes. It can be postulated that the oceanic species cannot withstand the temperature and salinity variations of the neritic region, and that *Sagitta friderici* cannot withstand the warmer oceanic waters to the west and south or the cold waters to the north of its range. Whether or not the distributions of the disjunct equatorial species (*Sagitta neglecta*, *S. pulchra*, and *S. bedoti*) can be accounted for by similar phenomena remains to be seen.

Sagitta minima Grassi and **Sagitta** sp. (**serratodentata** group)

(Figs. 21–22)

A second group of species that show poor agreement with the water masses live primarily between 100 and 300 meters. These are the mesoplanktonic species. In certain regions of reduced surface temperature these forms may be very abundant in the upper 100 meters. Typical of this group are *Sagitta minima* and *Sagitta* sp. (*serratodentata* group, possibly *S. serratodentata tasmanica* Thomson 1947).

Sagitta minima (Fig. 21) seems to inhabit the regions between water masses or the regions of mixing of the water masses. A few individuals are able to submerge under the edges of the warmer Eastern Pacific Central Water off the California Coast. Pierce (1953) has shown that in the western North Atlantic *S. minima* is most common in mixed water over the continental shelf.

Sagitta sp. (Fig. 22) shows a marked morphologic change in the region of 20° N. Lat., in apparent association with the faunal boundary there. It is possible that subspecies should be erected for the two populations, or they may actually be two separate species. If so, the two populations would be similar in distribution to *Sagitta friderici* and *S. bedoti* (Figs. 17–18), which are closely related. It seems likely that the extension of *Sagitta* sp. north into the California Current from the Pacific Equatorial Water is related to the Equatorial Water beneath the California Current at depths of 200 to 800 meters. Michael (1911) has shown that this species is most common off San Diego at 200 to 300 meters depth.

Sagitta decipiens Fowler, **Sagitta lyra** Krohn, **Krohnitta subtilis** (Grassi), and **Sagitta maxima** Conant

Although these species appear to belong to the second group, they were not adequately sampled on many of the expeditions listed in Table 1, either because of the small nets used or because the tows were not deep enough. Their distribution in the samples is so patchy that it is difficult to draw any conclusions from the data at hand. The northern boundary of *Sagitta minima* at 42° to 45° N. Lat. also seems to be the northern limit for *S. decipiens*, *Krohnitta subtilis*, and *Sagitta lyra*, and the southern limit of *S. maxima*.

Sagitta macrocephala Fowler, **Sagitta planctonis** Steinhaus[6], and **Eukrohnia fowleri** Ritter-Zahony

These three bathypelagic species, comprising a third group, occur chiefly below 500 meters throughout the Pacific as far north as 55°. As was previously mentioned, *Eukrohnia hamata* extends from the Arctic to the Antarctic and varies its depth from the surface to below 500 meters. *Sagitta planctonis* and *Eukrohnia hamata* are frequently found in the upper 300 meters of water in the Equatorial Water Mass.

Heterokrohnia mirabilis Ritter-Zahony

The abyssal-pelagic chaetognath, *Heterokrohnia mirabilis*, has been reported from the Antarctic, and recently from Kamchatka (Tchindonova 1955). It occurred in only one of the 3,000 samples discussed here, Shellback trawl no. 14 (from 11° 2′ N. Lat., 91° 46′ W. Long. to 11° 55′ N. Lat., 91° 32′ W. Long.) in a deep tow to 2,300 meters. This record shows that *H. mirabilis* is not a bipolar species as postulated by Tchindonova (1955), but is probably a cosmopolitan very deep water species.

[6] David (1956) recently revised the *Sagitta planctonis* group. In the present work all specimens of this group are provisionally considered one species, here called *S. planctonis*.

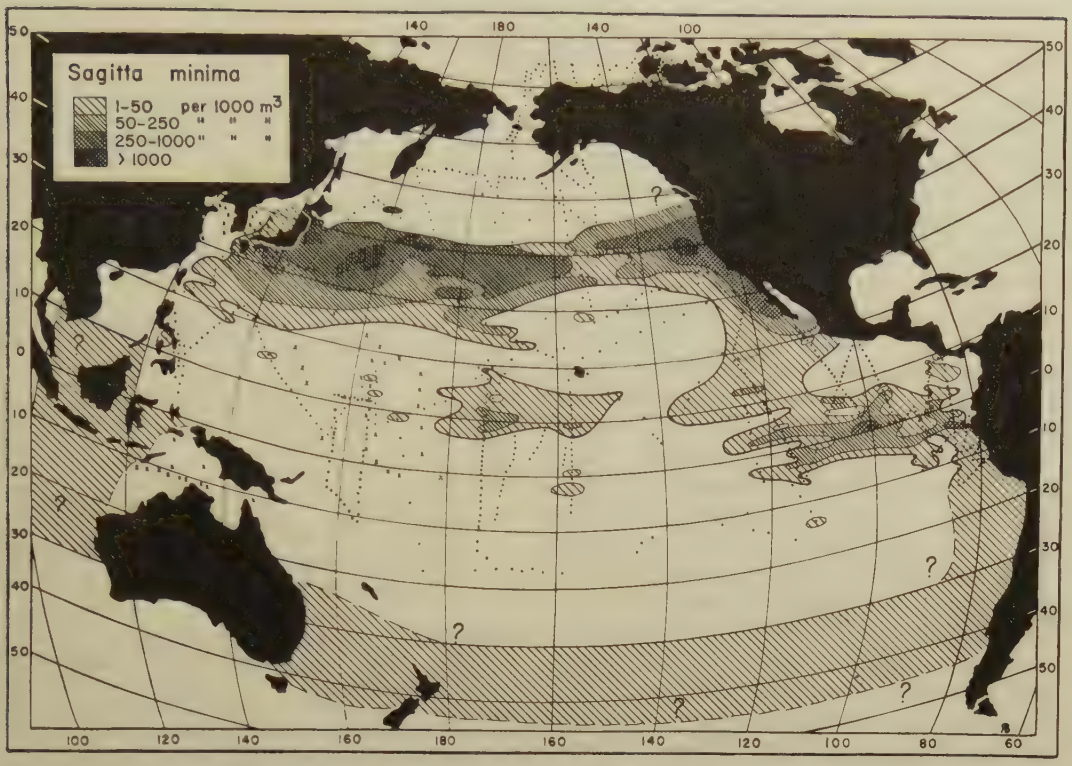

FIG. 21. Distribution of *Sagitta minima* in the Pacific. This species is most common in the regions of mixing of water masses. ×'s as in Figure 2. Distribution off eastern Australia is based on Thomson (1947).

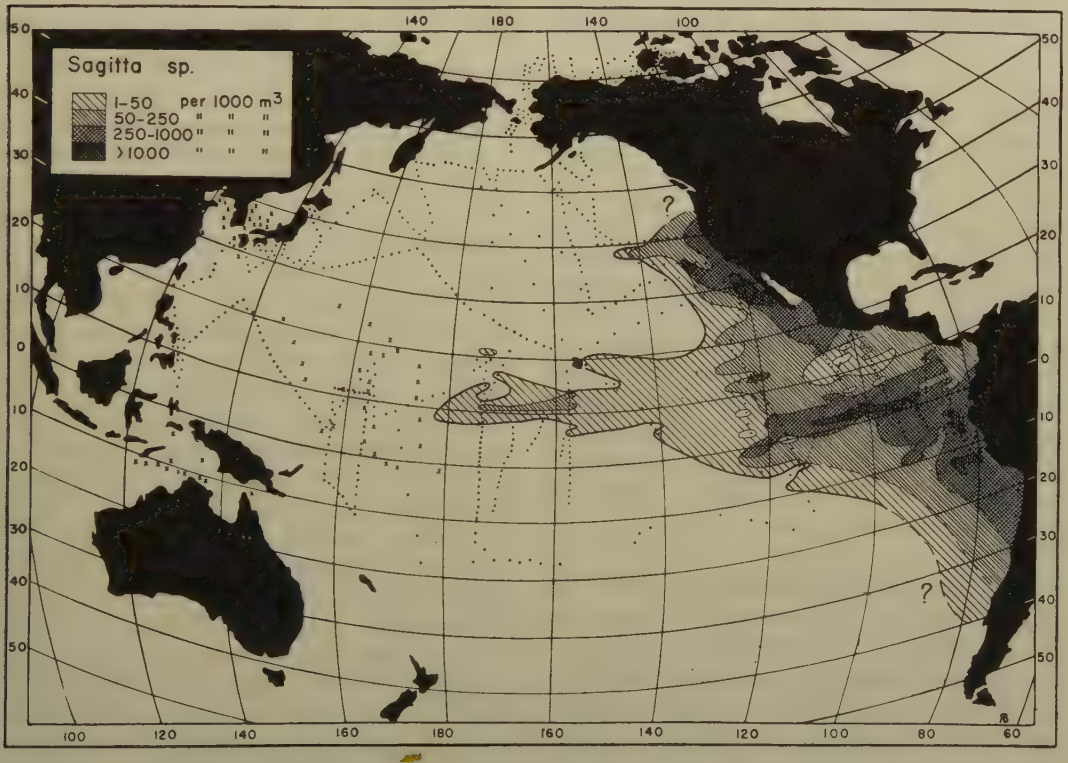

FIG. 22. Distribution of *Sagitta* sp. (*serratodentata* group) in the Pacific. ×'s as in Figure 2.

NATURE OF THE BOUNDARY REGIONS

The major part of plankton indicator work is concerned with changes in the geographic limits or boundaries of species and to a lesser extent with changes in relative proportions of various species and changes in the extent of the nursery grounds of species. In a study such as the present one, which encompasses as large an area as the Pacific, a comprehensive study of the boundaries can not be presented. Instead, a few of the techniques which may throw more light on this type of problem are pointed out.

In only a few places have the species boundaries been crossed frequently enough or at sufficiently close spatial intervals to permit even a preliminary analysis of seasonal changes and mixing processes in the boundary regions. The limit of *Sagitta pseudoserratodentata* south of Hawaii was traversed four times, twice in summer and twice in winter. On three of these traverses the southern limit was at 10° N. Lat., and on the fourth traverse it was at 9° N. Lat. There are only slight differences in the patterns of abundance as measured by running averages by two's (Fig. 23) between the lines at 172° and 158° W. Long.

Vertical profiles of temperature and salinity across this boundary at 172° W. Long. are shown in Figure 24. A layer of warm water between 12° N. Lat. and 3° N. Lat. and a dome of relatively cold water below are conspicuous features of the region. If it is postulated that *Sagitta pseudoserratodentata* can live only between temperatures of 18 and 26.5° C., then it would be confined to a narrow band of water 50 meters thick at 9° N. Lat. If this temperature range were responsible for its distribution, the species should reappear in good numbers south of 3° N. Lat. Its absence from this region may be due to the higher salinities in the upper 150 meters of water south of 6° N. Lat.

The concentration gradients, estimated from Figure 23 by eye and expressed as change per degree of latitude, vary from 4 to 5, the gradient decreasing irregularly but gradually from 20° N. Lat. On the other hand, the limit of the same species southwest of Baja California at 120° W. Long.,

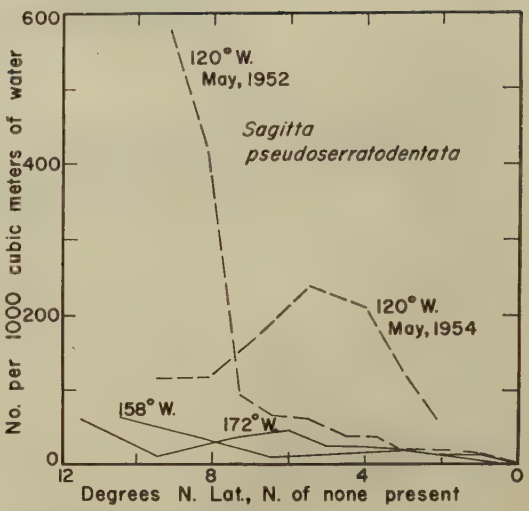

FIG. 23. Decrease in concentration of *Sagitta pseudoserratodentata* as the southern limit of its range is approached. The gradients at 158° and 172° W. Long. are about five specimens per 1,000 cubic meters of water per degree of latitude. At 120° W. Long. the gradients are of the order of 15 and 25. The sections at 158° and 172° W. Long. were made in June to August, 1950. Sections at 158° and 172° made in January to March, 1951, were about the same as those made in June to August, 1950.

on two crossings, had concentration gradients of 15 and 25 (Fig. 23). These compare with a concentration gradient of approximately 80 for *Sagitta elegans* north of Point Barrow (Fig. 3).

The concentration gradient can be used as a measure of the abruptness of the species limit and is greatest where a species is limited by a land mass. Off San Diego, for example, concentration gradients of *Sagitta friderici* near shore are frequently as high as 5000 in 60 nautical miles. The few comparisons that have been made indicate that changes in the gradients with time are less pronounced than are the differences due to geographic location.

Another measure of the strength of a boundary is the number of species that are limited by the boundary. In this respect the boundary southwest of Baja California is one of the most striking yet found in the Pacific. At least eight species of chaetognaths (*Sagitta pseudoserratodentata*, *S. robusta*, *S. ferox*, *S. pulchra*, *S. bedoti*, *S. neglecta*, *S. regularis*, and *Krohnitta pacifica*),

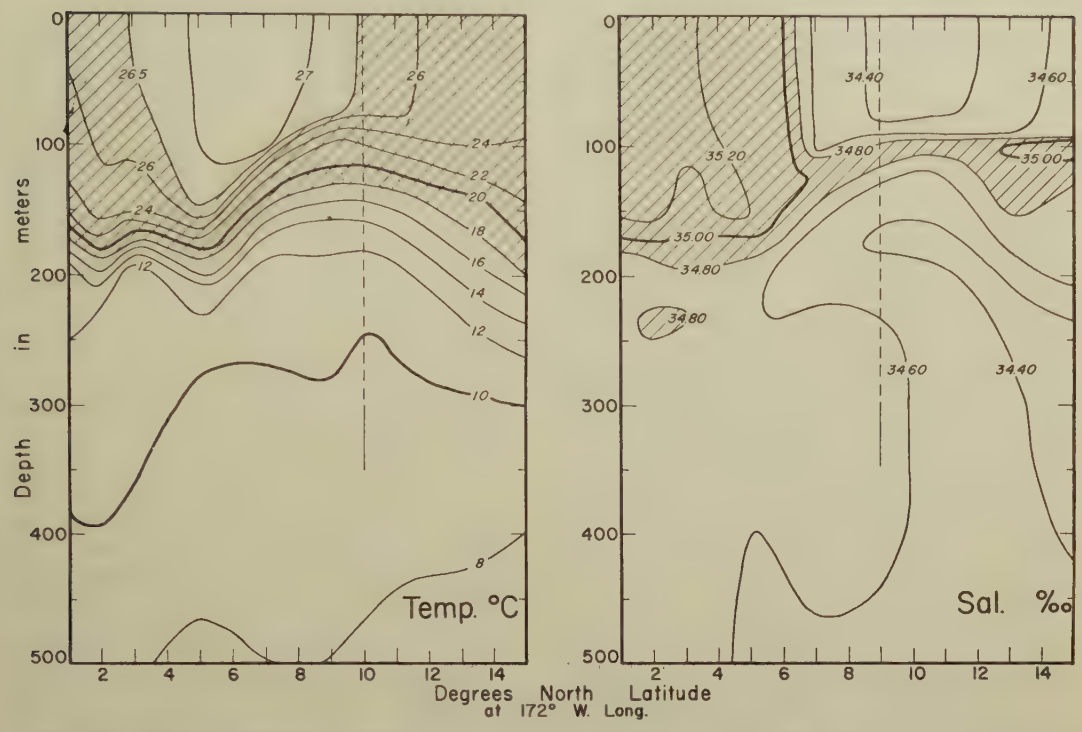

FIG. 24. Verti cal sections of temperature and salinity at 172° W. Long. (Fig. 1). The southern limit of *Sagitta pseudoserratodentata* at 10° N. Lat. is indicated by dashed lines.

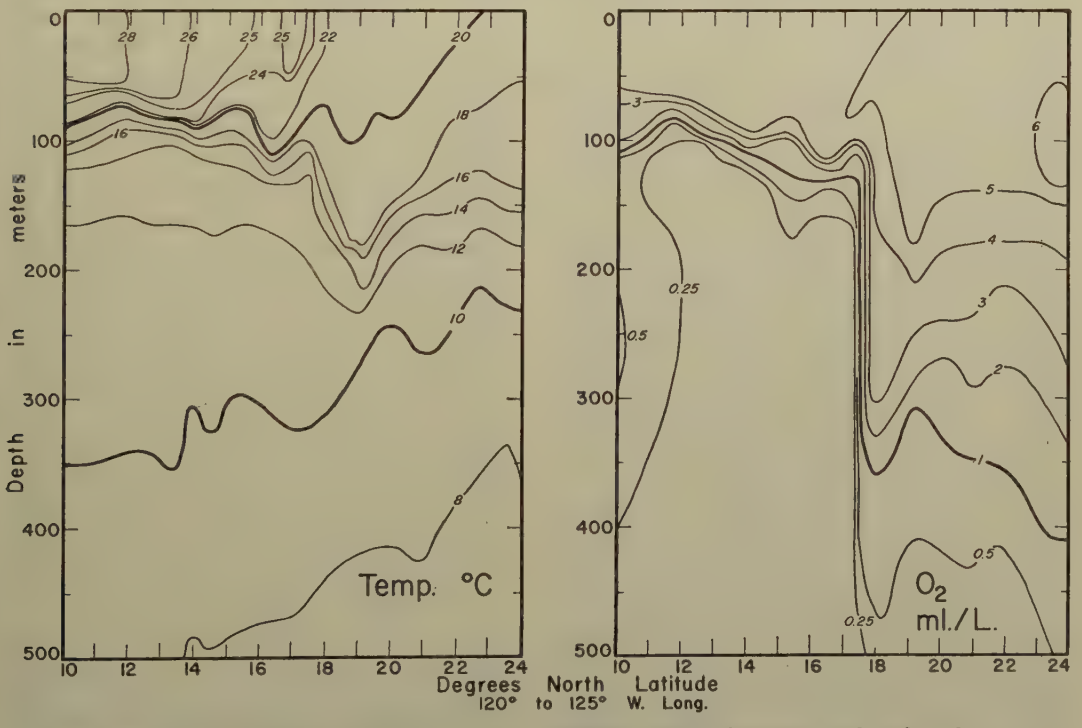

FIG. 25. Vertical sections of temperature and dissolved oxygen between 120° and 125° W. Long. (Fig. 1). The sharp gradients in temperature and especially oxygen at 18° N. Lat. are conspicuous.

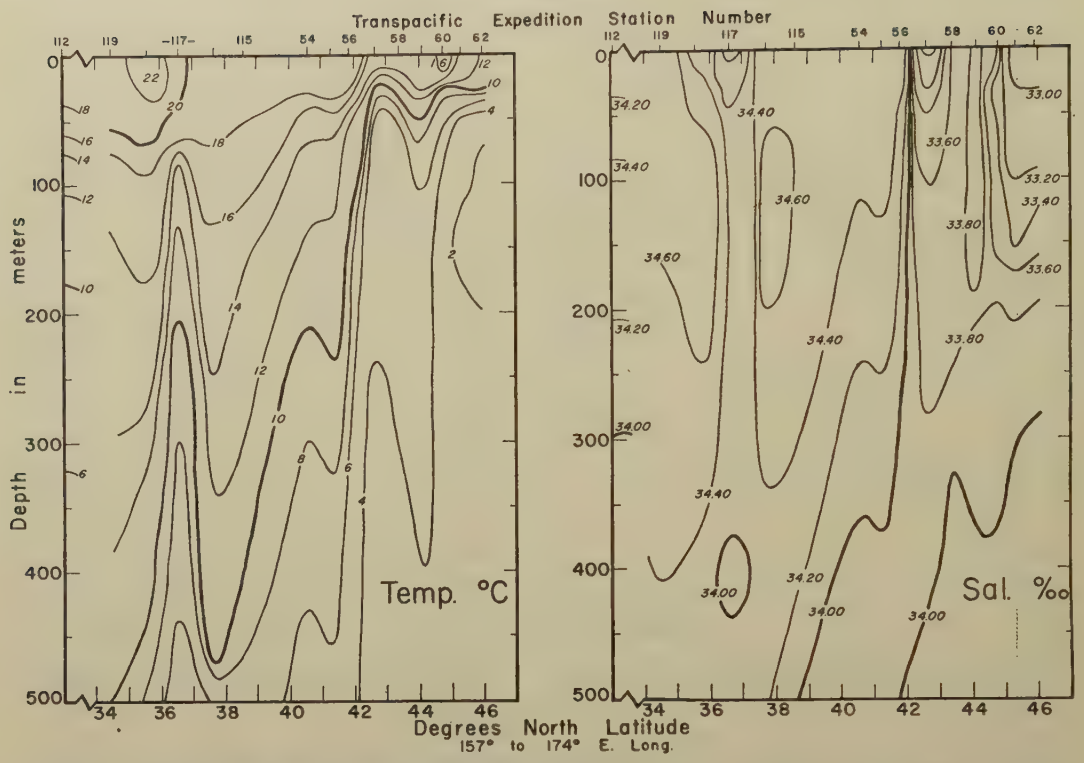

FIG. 26. Vertical sections of temperature and salinity in a section northeast of Japan (Fig. 1). Note the small pool of 16° C water in the upper 15 meters at 45° N. Lat.

one-third of those occurring in the region, have either a northern or southern limit there. This boundary is marked by a sharp temperature change at the surface between 17° and 18° N. Lat. as shown by the four isotherms (22–25°C.) that reach the surface there (Fig. 25). This temperature "wall" extends to a depth of at least 200 meters. The corresponding vertical section of oxygen concentration shows that there is a pronounced boundary extending at least as deep as 500 meters with very little mixing across the boundary. The oblique net tows available from Shellback Expedition when these sections were made, do not throw any light on the question of the relative importance of temperature, salinity, and oxygen in this boundary region.

The transport of expatriated communities across the subarctic barrier, presumably by large eddies, was discussed above. Vertical sections of temperature and salinity between Transpacific Expedition stations 62 to 54 and 115 to 119 illustrating this phenomenon are shown in Figure 26. The major feature of the region is the sharp slope of the isotherms and isohalines extending to more than 500 meters and separating cold, low salinity water to the north from warm, relatively high salinity water to the south. Station 60 (44° 46′ N. Lat., 159° 55′ E. Long.) has a thin layer of comparatively warm water in the upper 15 meters, and this is presumed to be the source of the warm water species taken at this station.

Station 112 (36° 35′ N. Lat., 163° 46′ E. Long.) had *Sagitta elegans* present in a tow from 160 to 280 meters deep. The T-S diagram from this station indicates that only Pacific Central Water was present in this depth range. *Sagitta elegans* may have persisted in this water until it lost all of its subarctic character. It is also possible that the net tow sampled water with temperature-salinity characteristics different from that sampled by the hydrographic cast since the two observations were not simultaneous.

With the development of a technique for microscopically examining zooplankton at

sea (Bieri 1956), it is now possible to sample selected boundaries at very close intervals of time and space. A synoptic approach should lead to a better understanding of the mechanisms that tend to mix separated populations and permit detailed studies of population structures in the different boundary regions.

COMPARISON WITH THE DISTRIBUTION OF OTHER PLANKTON ORGANISMS

Although it has long been known that there are characteristic plankton communities in the sea, these communities have been worked out in only a few restricted regions, chiefly parts of the North Atlantic. In attempting to determine the primary cause or causes of the species limits, it is important to compare the distributions of the chaetognaths with those of other zooplankton organisms, especially those with a different mode of nutrition, and to phytoplankters which in addition to different nutritional requirements have a vastly different method of reproduction and rate of growth. If the species barriers or limits are in general the same for many different groups of organisms, then any explanation of the cause of the species limits must explain not only those for the chaetognaths, but also those for the other animal and plant groups. Although the distribution of each species of chaetognath is unique in itself, certain similarities between various species have been pointed out in the discussion of distribution patterns. These general types of distribution are similar to the distribution of other animal species.

Most previous observations in the Pacific have been so scattered and far apart that it is difficult to establish the range or limit of any species. However, where sampling has been detailed, the other zooplankton groups coincide fairly well with the distributions of the chaetognath species. For example, Bowman (1955) described a new species, *Calanus lighti*, which has a distribution off California and Baja California that is typical of the cosmopolitan warm-water species. However, *C. lighti* is absent from the eastern equatorial Pacific and is apparently a central species similar in distribution to *Sagitta pseudoserratodentata*.

Boden, Johnson, and Brinton (1955) delimit the generalized distributions of the Pacific euphausiids. *Nyctiphanes simplex*, near shore in the California and Peru Currents, is similar in distribution to *Sagitta friderici*. The range of *Euphausia recurva* is split into a north and south central population, similar to, but more pronounced than the anti-equatorial distribution of *Sagitta californica*. *Euphausia tenera* is an equatorial-west-central species similar to *Sagitta robusta*. *Euphausia hemigibba* is largely restricted to the North Pacific Central Water (*Sagitta pseudoserratodentata*), while *Euphausia gibba* is restricted to the South Pacific Central Water.

In their study of the very extensive Carnegie material, Graham and Bronikovsky (1944) charted the occurrences of 52 species of the genus *Ceratium* and thus provided comparative material. On the basis of these species distributions, the Pacific and Atlantic were each divided into a cold and warm region at about 40° N. Lat., similar to what has been shown in this paper for the chaetognaths. Off the coast of South America the authors established a southeast Pacific region that appears to be a delineation of the Eastern South Pacific Central Water. Many of the *Ceratium* species appear to be similar to the Chaetognatha in distribution.

Their Chart 2 (Graham and Bronikovsky 1944, p. 187) for *Ceratium cephalotum* shows a distribution similar to that of *Sagitta californica* and *Euphausia recurva*, occupying the North and South Central Water, but apparently excluded from the Peru and California Currents and the Equatorial Water Mass. *Ceratium belone* also seems to have an anti-equatorial or perhaps wider antitropical distribution. *Ceratium gravidum*, *C. candelabrum*, *C. pulchellum*, *C. semipulchellum*, *C. massiliense*, *C. contorticum*, and at least seven or eight other species of the genus are widespread, warm-water species similar to *Sagitta enflata*. *Ceratium filicorne* appears to be restricted to the Pacific Central Water. *C. deflexum* is an equatorial-west-central species absent from the Eastern North Pacific Central Water, as is *C. lunula*. Graham and Bronikovsky suggest that, "It is possible

that the slight variations in salinity found in the oceanic waters have no influence on the distribution of *Ceratium* species." They point out that the limit of the warm and cold water provinces in the Atlantic is at a surface salinity of about 36‰, whereas in the Pacific the same species are limited at a surface salinity of 33 to 34‰. On the other hand, the correlation with temperature is rather poor. The distribution of *C. lunula* (their Chart 31, p. 197) shows poor agreement with surface temperature. However, the limits of this species do agree quite well with the extent of the water masses as defined by temperature and salinity combined. *Ceratium tripos atlanticum* may be similar in distribution to *Sagitta friderici*. The eastern neritic temperate species such as *Sagitta friderici*, *Nyctiphanes simplex*, and *Ceratium tripos atlanticum* are associated with upwelling water in the Peru and California Currents and give these currents unique faunas.

As was pointed out in the discussion of the distribution of *Sagitta robusta*, the Eastern South Pacific Central Water is very similar to the Equatorial Water in its temperature and salinity relationships. It is interesting that Graham and Bronikovsky's data show three equatorial-west-central species—*Ceratium breve*, *C. incisum*, and *C. lunula*—that are absent from the Eastern South Pacific Central Water, and three other equatorial-west-central species—*C. deflexum*, *C. reflexum*, and *C. falcatum*—that occur in the Eastern South Pacific Central Water.

DISCUSSION

Each of the upper water masses of the Pacific has a unique temperature-salinity regimen that is brought about in large part by the oceanic currents. For example, large horizontal current gyres in the Subarctic and Central Water Masses tend to maintain the relatively small range of temperature-salinity values found in these waters. The oceanic circulation, which allows some lateral mixing between the water masses as shown by the temperature-salinity relationships, also tends to keep various animal populations isolated from one another. On the other hand, the upper water masses are defined on the basis of the temperature-salinity relationships found below 100 meters, because comparatively large seasonal changes and other variations in temperature and salinity confuse the interpretation of lateral mixing in the surface layers.

In the preceding presentation the apparently close relationship of species limits to water mass boundaries has been emphasized. Although the postulated relationship may be spurious, there are three possibilities which may justify such comparisons even though it is apparent that most of the species discussed have their greatest abundance in the upper 100 meters.

First, even though the majority of the species are most abundant above 100 meters, all of them extend at least as deep as 200 meters, and many of the warm water species such as *Sagitta enflata* have been reported from as deep as 500 meters. Thus it is possible that as a population approaches a boundary region, the surface-living individuals are eliminated first and the deeper-living individuals would then define the total range.

Secondly, the upper-living (epiplanktonic) species are capable of some submergence when unfavorable conditions are encountered in the surface layers. Although this is especially true when a species encounters water warmer than it can tolerate, in some regions relatively high salinity, high temperature water may be carried beneath colder, less saline surface waters. In such localities and where submergence is possible the T-S relationships of the water masses would reflect the environment of the species limits.

Finally, the fact that there appears to be good agreement between species limits and water-mass boundaries would indicate that the temperature-salinity relationships below 100 meters, which define a water mass throughout the greater part of its extent, also occur at the surface in the boundary regions. This is known to be the case in certain regions where the water masses are formed, as for example northeast of Japan where the Oyashio and Kuroshio Currents meet and give rise to the Intermediate and North Pacific Central Water Masses. Al-

though extensive studies of seasonal temperature variations in the upper 100 meters of water have been made in recent years following the advent of the bathythermograph, seasonal studies of temperature and salinity together on a broad scale are not yet available. The detailed examination of these possibilities by future expeditions will either confirm or negate the implied causal relationship between species limits and temperature-salinity.

Knowing the distributions that have been presented, it is possible, on the basis of the chaetognath species present, to locate quite closely the locality from which a plankton sample has been taken, provided that the tow is oblique from the surface to 300 meters, and the net large enough to take a sufficiently large and reliable sample. For example, the presence of *Sagitta elegans* would place a sample north of 40 degrees, or, if *S. decipiens* were absent, north of 45 degrees. The North Pacific Central Water can be distinguished by the presence of *Sagitta pseudoserratodentata*. The absence of *S. robusta* and *S. regularis*, with *S. pseudoserratodentata* present, would show that the sample came from the Eastern North Pacific Central Water. The absence of *S. pulchra*, *S. neglecta*, *S. bedoti*, and *S. pseudoserratodentata*, with *S. robusta*, *S. regularis*, and *Krohnitta pacifica* present, would place the sample in the oceanic region of the Equatorial Water Mass. The presence of *Sagitta pulchra*, *S. bedoti*, and *S. neglecta* would place the sample in the east or west "neritic" Equatorial Water, while the presence of *Sagitta* sp. would show that the sample came from the eastern "neritic" Equatorial Water. The presence of *S. friderici* would place a sample off the coast of North or South America. Although the ability to predict the location from which a sample has been taken may have no oceanographic or practical application, it does give an indication of the relative state of knowledge of the animal group.

It is thus apparent that every region of the Pacific has a distinctive chaetognath fauna, though the chaetognaths in any local fauna are but small parts of large, widespread populations. In some regions the species composition may change very little with time. On the other hand, qualitative changes may occur quite rapidly when a locality has a species boundary through it. In certain regions, as off the coast of Baja California, the species may come from two or three different faunas with only one or two species endemic to the locality. In such places a change in the total zooplankton population can only be predicted by knowing the relative importance of the contribution of each fauna.

The North Pacific Subarctic Convergence has been recently discussed by many Japanese and Russian investigators, for instance Brodskii (1952, 1955), Bogorov and Vinogradov (1955). The Convergence separates the Subarctic and Central Water Masses at 40° to 45° N. Lat., and is the region of a major barrier for the phytoplankton as well as the zooplankton. It is regarded as a division between two of the three great provinces of the Pacific, the northern cold-water province, and the warm-water province. Nevertheless, it is not a sharp boundary in that many of the warm-water species disappear short of the convergence, and many others do not disappear until they have been carried several degrees beyond the convergence. This is particularly true of the deeper-living species. The effectiveness of the subtropical convergence and the subarctic convergence in the Atlantic in limiting pelagic species is well established, and it seems highly probable that the Pacific subtropical convergence at about 40° S. Lat. will be shown to be an equally formidable barrier to many species of Chaetognatha.

The agreement between the species distributions and the water masses is best in the Eastern Pacific, though this may be partly due to the fact that sampling with large nets has been more intensive in the Eastern Pacific. Thus the pelagic species are most sharply separated into different populations in the eastern half of the ocean, where in general the currents are more sluggish. It appears that the slower currents allow more permanent temperature and salinity discontinuities to form and also do not displace populations so far before they are eliminated by adverse environmental factors.

Spatial variations in the concentration of the various species appear to be primarily

due to the basic productivity of the local areas that constitute the total distribution. Thus, *Sagitta pseudoserratodentata* (Fig. 12) is most abundant along the edges of its range, where there is a higher standing crop of phytoplankton and zooplankton, than in the interior of the Pacific Central Water, where its concentration appears to be less than one individual in 3000 cubic meters of water. The rapid decrease in abundance of the *S. friderici* population off California, already mentioned, is correlated with a decrease in the standing crop of phyto- and zooplankton. Thus it seems that species abundance is dependent on three major variables—temperature, salinity, and available food as indicated by standing crop.

FUTURE WORK

The present study is based on a very sensitive sampling technique wherein a single specimen may be recovered from 1,000 cubic meters of water, or a sensitivity of about one part in 10^{13} by volume. Yet this sensitivity is not enough. By increasing the net diameter to two meters and by doubling the length of tow it would be possible to increase the sensitivity by almost one order of magnitude. Such a procedure is absolutely essential in the barren Pacific Central Waters if statistically reliable differences are to be demonstrated.

The available plankton samples do not allow a detailed study of time changes in the species limits and concentrations. Where repetitive sampling has been carried out, changes with time have been pointed out.

Subspecific variation has been considered briefly in the discussion of *Sagitta* sp. (*serratodentata* group). Even such well known species as *S. enflata*, *S. hexaptera*, and *S. decipiens* show marked morphologic variations in different parts of their range. The detailed study of these variations should lead to a better understanding of the requirements that the environment imposes on the various species, and should give some clues as to how temperature and salinity are connected to the physiology of the species in limiting its distribution.

The extensive material that has been examined for this work still leaves large gaps in our knowledge of the horizontal, and especially the vertical, distribution of the various species. The water masses are still incompletely defined in many regions, and this may account for some of the discrepancies between the species distributions and the water masses. Most of the expeditions took only oblique net tows so that exact correlation with temperature and salinity is not possible. Despite these great handicaps, with the populations as outlined above as a frame of reference it is now possible to make quantitative vertical sections of the chaetognath fauna and various physical-chemical parameters in local areas and to relate such observations more exactly to the huge moving system, the ocean.

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A Change in the Early Growth Rates of Four Larval Marine Fishes[1]

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ABSTRACT

The growth curves (age on length) of four widely diversified species of fish larvae (*Sardinops caerulea, Pleuronichthys verticalis, Tetragonurus cuvieri,* and *Trachurus symmetricus*) were divided into three sections: A, B, and C. Growth in Section A is very rapid but of short duration. Growth in Section B is much slower but of longer duration. Section C follows absorption of yolk materials and chronicles the rate at which the larvae metabolize themselves. The growth curves for several other species of fish derived from data given in the literature are generally in agreement with those derived by more rigorous analysis. The slopes of Section A were compared with Section B for each fish. These ratios lie between 4 and 10. The effect of non-logarithmic growth on estimates of larval survival is discussed.

INTRODUCTION

The purpose of this paper is to report a change in rate of increase in length as correlated with time for the larvae of four marine fishes.

The importance of vital statistics, *i.e.*, birth, growth, and death rates, was realized very early in the development of fishery biology. In the past fifty years many vital statistics have been collected for adult fishes. These data have proved invaluable in the quantitative approach to fishery ecology. However, the quantitative ecologist has been somewhat hampered in his studies by the paucity of data (*i.e.*, vital statistics) for the younger stages. The chief reason for this lack of data for younger stages is the difficulty encountered in making suitable observations.

Growth rates are customarily estimated by following length-frequency modes through time. This procedure usually gives reliable information. However, as the rate of growth increases, the interval between samplings must be shorter so that changes in rate may be properly estimated. This requirement may preclude the use of the length-frenquency method in marine environments where ship time and money are limited. Therefore, a fish egg incubator was devised so that direct observations could be made under conditions of controlled temperature.

The study was undertaken primarily to obtain data on jack mackerel growth. These data are to be used in the estimation of early survival described below. The other fish, which were taken in jack mackerel samples, were studied in order that a comparison of growth rates might be made.

METHODS

Fish eggs were taken directly from the sea (temperature 15°C) with a plankton net. They were sorted by species and stage of development into jars of fresh sea water. The jars were then capped and placed in the incubator, which had been set at 15°C (accuracy ± 0.2°), a temperature which seems optimal for at least two of the species, jack mackerel and sardine. Daily observations were made of the stage of development until hatching. After hatching, the lengths (snout to tip of tail) of the larvae were measured daily by means of an ocular micrometer. The number of observations per day varied because the fish were examined in the open. The air temperature variation between cloudy and sunny days caused a variable warming of the fish during the period when the fish were measured. The fish warmed faster on

[1] Dr. E. H. Ahlstrom has aided in the collection and identification of the fish eggs and larvae; A. M. Vrooman, George Mattson, Frank Reid and Ruben Lasker have aided in the collection of fish eggs. Mr. Bruce Taft assisted with the statistical analysis.

sunny days, and fewer fish were measured to prevent sharp temperature changes. The fish were observed from shortly after the time they were spawned in the sea until they died. No attempt was made to feed them. In nature feeding probably starts about the time of yolk sac absorption. An average length for each species was computed for each day. At the conclusion of the experiment, the lengths were transformed to logs, and lines were fitted by the least squares method (Y = length; X = day; $\log Y = a + bX$).

TABLE 1. *Sardine growth in mm*

	Days past hatching							
	0	1	2	3	4	5*	6	7
Lengths	3.0	4.2	4.4	4.4	5.1	4.9	4.7	4.9
	3.1	3.6	4.4	4.4	5.3	5.1	4.7	5.1
	3.4	4.2	4.7	5.1	5.3	5.3	4.9	5.1
		3.8	4.5	4.9	5.3	5.6	4.9	4.7
		4.4	4.7	4.5	5.3	5.2		4.7
		3.5	4.5	5.3	5.1			
		4.0	4.8	5.3	5.1			
		3.9	4.7	4.8	5.1			
		3.6	4.3	4.7	4.7			
		3.5	5.1	4.9				
		3.6	4.5	4.4				
		3.6	4.7					
		3.6	4.9					
		3.6	4.7					
		3.6	5.1					
		4.0						
		4.2						
		4.5						
		4.5						
		4.4						
Average length	3.2	3.9	4.7	4.8	5.1	5.2	4.8	4.9
Log average length	.505	.591	.672	.681	.707	.716	.681	.690

* Yolk sac absorbed.

RESULTS

The basic growth data are given in Table 1 for the Pacific sardine, *Sardinops caerulea* (Girard); in Table 2 for the hornyhead turbot, *Pleuronichthys verticalis* Jordan and Gilbert; in Table 3 for the squaretail, *Tetragonurus cuvieri* Risso; in Table 4 for the jack mackerel, *Trachurus symmetricus* (Ayres).

Plots of the daily average lengths (Fig. 1) suggested that the curve for each species might be more accurately represented by three curves. For example, during the first two days of larval life the sardine grew about 0.8 mm per day. During the next three days it grew about 0.2 mm per day, and during the last two days it shrank about 0.1 mm per day. The growth rates within periods were more uniform than the growth rates between periods. Data for each section of the curve for each species of fish were grouped together because of their within-section uniformity and their apparent differences from data of adjacent sections.

Section A includes the first one to three

TABLE 2. *Turbot growth in mm*

	Days past hatching										
	0	1	2	3	4*	5	6	7	8	9	10
Lengths	3.1	3.8	4.0	3.6	4.0	3.6	4.0	3.1	3.7	3.8	3.8
		3.8	3.8	3.9	4.0	3.7	4.1	4.1	3.7	4.0	4.4
		3.8	3.8	3.9	4.0	3.6	3.6	3.8	4.0	3.8	4.2
		3.6	3.8	3.8	4.2	3.7	3.8	3.7	3.5	4.4	
		3.8	3.8	3.8	4.2	4.4	3.6	3.8	3.8	4.2	
		3.7	3.8	3.8		3.9	3.5	4.0	3.8		
						4.0	4.4	4.4	4.3		
							4.3	4.4	4.4		
							4.4		4.1		
									4.4		
									4.3		
									4.4		
Average length	3.1	3.8	3.8	3.8	4.1	3.8	4.0	3.9	4.0	4.0	4.1
Log average length	.491	.579	.579	.579	.612	.579	.602	.591	.602	.602	.612

* Yolk sac absorbed.

TABLE 3. *Squaretail growth in mm*

	Days past hatching													
	0	1	2	3	4	5*	6	7	8	9	10	11	12	13
Lengths	3.2	3.6	3.5	3.9	4.7	4.5	4.5	4.4	4.5	4.5	4.4	4.5	4.4	4.4
	3.3	3.6	3.7	3.7	3.8	4.4	4.9	4.5	4.9	4.5	4.5	4.5	4.4	4.0
	3.0	4.2	3.8	3.8	4.7	4.7	4.5	4.7	4.7	4.7	4.7	4.5	4.4	4.1
		4.0	3.9	4.4	3.8	4.5	4.5	4.5	4.4	4.7	4.7	4.4	4.8	
			4.4	4.4	4.4	4.9	4.8	4.6	4.4	4.9	4.7	4.4	4.5	
			4.4	4.0	4.2	4.5	4.6	4.5	4.5	4.7	4.7			
			4.4	4.0	4.4	4.9	4.4	4.4	4.7	4.7	4.9			
			4.4	3.9	3.8	4.7	4.6	4.6	4.9	4.5	4.7			
			4.9	4.0	5.3	4.9	4.7	4.5	4.9	4.7	4.7			
			4.3	4.4	4.7	4.7	4.5	4.7	4.5	4.7	5.1			
				4.8	3.5	4.5	4.5	4.9	5.1	4.7	5.3			
				4.4	4.7	4.6	4.2	4.7	4.7	4.9				
				4.9	4.7	5.1		5.1		4.9				
				4.5	4.9	4.4		4.5						
				4.4	4.9			4.5						
				4.7	5.8			4.7						
				4.7	4.5									
				5.1	4.4									
Average length	3.2	3.9	4.2	4.3	4.5	4.7	4.6	4.6	4.7	4.7	4.8	4.5	4.5	4.2
Log average length	.505	.591	.623	.633	.653	.672	.662	.662	.672	.672	.681	.653	.653	.623

* Yolk sac absorbed.

TABLE 4. *Jack mackerel growth in mm*

	Days past hatching											
	0	1	2	3	4	5	6*	7	8	9	10	11
Lengths	2.0	2.6	2.9	3.6	3.3	3.3	3.8	3.6	3.6	3.6	3.2	3.4
	2.0	3.2	3.2	3.2	3.6	3.5	3.6	3.8	3.8	3.9	3.6	3.4
	2.0	2.9	3.0	3.2	3.3	3.6	3.6	3.8	3.8	3.5	3.6	
	1.9	2.9	2.7	3.1	3.5	3.6	4.1	3.8				
		2.4	2.7	3.5	3.5	3.5	3.6	3.8				
		2.8	2.8	3.3	3.5	3.6	3.6	3.8				
		2.6	2.8	3.2	3.5	3.6	3.7	3.8				
		2.7	3.1	3.3	3.2	3.4	3.8					
		2.2	2.8	3.2	3.7	3.6	3.5					
		2.1	3.0	3.4	3.5	3.7						
		2.4	3.1	3.6		3.3						
		2.4	3.1	3.6								
		2.6		3.3								
		2.2		3.5								
		2.9										
		2.2										
		2.9										
Average length	2.0	2.6	2.9	3.4	3.5	3.5	3.7	3.8	3.7	3.7	3.5	3.4
Log average length	.301	.414	.462	.531	.544	.544	.568	.579	.568	.568	.544	.531

* Yolk sac absorbed.

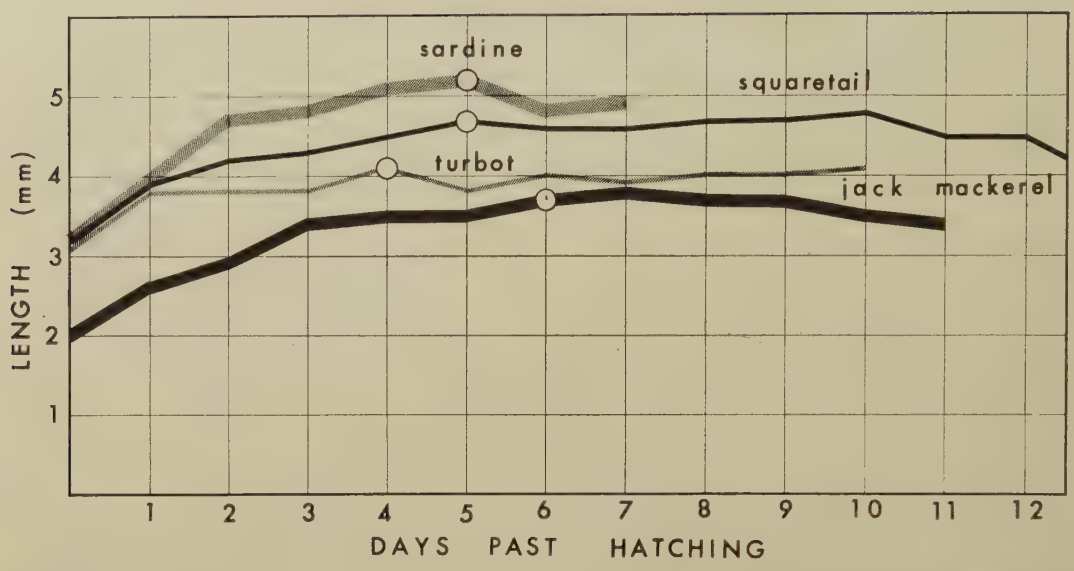

FIG. 1. Plot of daily average lengths (mm) of four larval marine fishes. 0 = day yolk sac is absorbed.

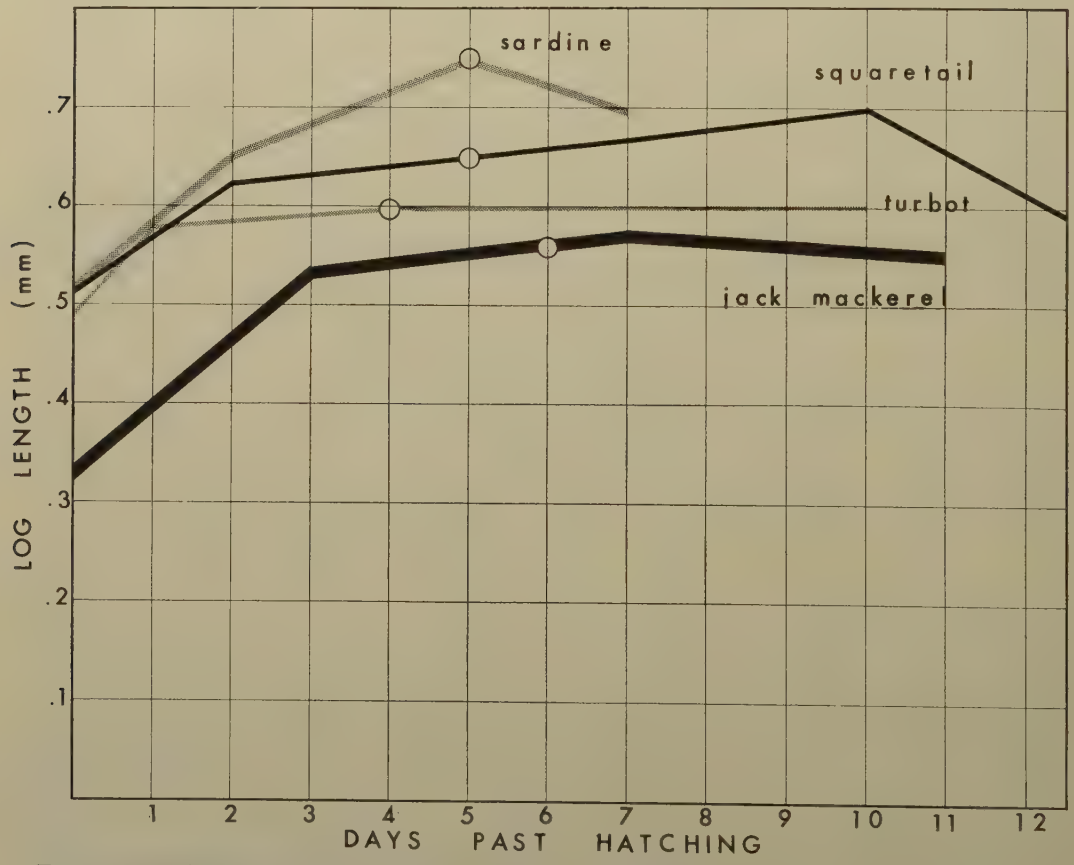

FIG. 2. Logarithmic growth curves of four larval marine fishes. 0 = day yolk sac is absorbed.

days of growth and is characterized by its relatively steep slope. Section B represents growth during the remainder of the week and has a much reduced slope. Section C represents the stage of growth after the absorption of the yolk and oil globule and extends to death. The mean slope is often negative. The presumed cause of the shrinkage in length is the consumption of body tissue by the larvae, but no special study has been made of this portion of the data. The age in days of fish during each section of the growth curve is given below:

	Section		
	A	B	C
Sardine	0–2	2–5	5–7
Turbot	0–1	1–4	4–10
Squaretail	0–2	2–10	10–13
Jack mackerel	0–3	3–7	7–11

The data did not reveal any uniform arithmetic growth rate. The curvature resulting from fitting together Sections A and B did not suggest logarithmic growth. Each section of each curve was treated separately by transforming the data to logarithms and then fitting least-square lines to the sections (Fig. 2 and Table 5). The log transformations were made solely so that these data would be in a form comparable to that used by Sette (1943) and Ahlstrom (1954).

The data were further analyzed by regression analysis. The homogeneity of variance among days was tested (Table 6) by a method described by Thompson and Merrington (1946). If there is a common variance, the probability distribution of M is known and can be used to test the hypothesis that the variances are equal. The variance cannot be shown to be equal for Section A of jack mackerel or Section B of squaretail. This is a violation of a basic assumption of the regression model so that the slopes cannot be rigorously tested. Assuming that more data would tend to equalize the variance without materially altering the estimate of the slope, estimates of the standard deviation of the slope (s_b) and spread about the regression line ($s_{y/x}$) are given (Table 5). The variances (if of the proper magnitude) indicate that the slopes of Section A are different from Section B, and that the slopes of Section B are different from zero.

TABLE 5. *Growth parameters*

	a	b	s_b	$s_{y/x}$	Ratio A/B slopes	Day section stops	Day yolk absorbed
Sardine							
Section *A*	.51	.081	.0087	.0103	4.5	2	5
Section *B*	.63	.018	.0011	.0748		5	
Turbot							
Section *A*	.49	.088	—	—	8.8	1	4
Section *B*	.56	.010	.0024	.0130		4	
Jack mackerel							
Section *A*	.33	.067	.0091	.0616	5.2	3	6
Section *B*	.49	.013	.0017	.0184		7	
Squaretail							
Section *A*	.51	.055	.0120	.0126	9.2	2	5
Section *B*	.62	.006	.0014	.0387		10	

The within-class variance in length of the sardine regressions are homogeneous so that regression analysis can be rigorously applied. The slope of Section B which has been interpreted as the relative growth rate through larval life may be compared with the slope derived by Ahlstrom (1954). His data were drawn from older larvae, and the growth rate was approximated by following a length-frequency mode through time. Ahlstrom obtained a slope of 0.019, which is within one standard deviation of the slope obtained from direct measurement for Section B. The Type II Error was computed to approximate the probability that in using the procedure described above the slopes would be called equal when they are really different. In order to do this, the slope computed by Ahlstrom was used as a known value without sample variation. By means of the power curve for the t test, it was determined that a difference of 0.001 between the hypothetical mean (Ahlstrom's figure) and the true mean (unknown in this case but estimated by the sample value) would not be detected about 30% of the time for $\alpha = 0.05$. The good agreement between methods suggests that the "natural" growth rate has been approximated.

The variable variances associated with the Sections A may be eliminated by shortening the interval between measurements and taking the same number of measurements for each time unit. However, the argument

TABLE 6. *The homogeneity of class variance*

	Class variance											Section A			Section B		
	0	1	2	3	4	5	6	7	8	9	10	$\bar{X}$	log $\bar{Y}$	$\bar{M}$	$\bar{X}$	log $\bar{Y}$	$\bar{M}$
Sardine	.0008	.0015	.0005	.0010	.0003	.0005						1.3	.614	5.994	3.1	.687	3.710
Turbot	.0000	.0001	.0001	.0002	.0001							1.0	.655	—	2.4	.585	5.740
Jack mackerel	.0001	.0029	.0007	.0005	.0004	.0003	.0004	.0001				1.8	.449	17.842	4.7	.547	8.297
Square-tail	.0004	.0011	.0020	.0020	.0030	.0004	.0003	.0003	.0004	.0002	.0005	1.4	.589	1.887	5.8	.656	53.865

that relative growth during the first few days is more rapid than later growth would not be changed. The length distribution of the dead larvae was not examined since the larvae are rapidly destroyed by bacteria. If there is a correlation between length and mortality, then a bias will exist.

Further suggestions of a change in growth rates may be found in Table 7. These data have been derived from various published sources. Embody's (1910) data (from Sette 1943) were transformed before they were regressed as described above. Some growth data were obtained from figure legends published by various authors (see References) in "Memoirs of R. Comitata Talassografico Italiano." The legends often give the age in days and the length in millimeters of the larvae. The lengths were transformed to the log scale, and the slope was calculated by the two-point formula

$$b = \frac{\left[\begin{matrix}\text{log length (mm)}\\ \text{of older larvae}\end{matrix}\right] - \left[\begin{matrix}\text{log length (mm)}\\ \text{of younger larvae}\end{matrix}\right]}{\left[\begin{matrix}\text{age in days}\\ \text{of older larvae}\end{matrix}\right] - \left[\begin{matrix}\text{age in days}\\ \text{of younger larvae}\end{matrix}\right]}$$

It will be noted that, in general, the magnitude of A slopes given in Table 7 is the same as that given in Table 5. However, three species in Table 7 have atypically large A slopes, and two of the three have significant deviations of the A/B ratio from the normal range of values of 2 to 10 (see below).

In order to assess the magnitude of the change in slope, a ratio of slope A to slope B was calculated for each species studied. This datum indicates that the initial growth is from about 2 to about 10 times that of the second period. Since the fish are subsisting entirely on the yolk during these intervals, these rates should approximate those found in nature.

TABLE 7. *Growth parameters*

Species	Slopes			Day Section *A* terminates	Source
	A	*B*	*A/B*		
Esox lucius	.053	.015	3.5	5	Sette (1943)
Mugil chelo	.012	.001	10.0	8	Sanzo (1936)
Plamys sarda	.013	.004	3.3	2	Sanzo (1932b)
Scorpoena sp.	.028	.006	4.9	5	Sparta (1928)
Pagellus centrodontus	.019	.004	4.7	3	Gaetani (1934)
Smaris insidiator	.076	.010	7.5	2	Sanzo (1939)
Orcynus thynnus	.102	.002	51.0	1	Sanzo (1932a)
Mora mediterranea	.125	—	—	1	Gaetani (1929)
Brama raji	−.116	.003	−38.6	0.5	Sanzo (1928)
Echelus myrus	.047	—	—	4	Sparta (1940)
Scarus cretensis	.088	—	—	2	Cipria (1939)
Seriola dumerilii	.034	.020	1.7	2	Sanzo (1933)

Although the growth rate has been approximated by two discontinuous log curves, a more detailed study would probably reveal a nonlogarithmic continuous growth function.

DISCUSSION

The four fishes intensively examined in this study are representatives of four evolutionarily diverse groups of fish. They all inhabit the coastal waters of southern California, and they all lay pelagic eggs. When a similarity, such as the A/B ratios, is observed among groups which are systematically divergent but ecologically related, the event, *i.e.*, change in slope, may be interpreted as a general adaptation to this particular mode of life. Or, alternatively, the change in growth rate may be a character-

istic of all fish larvae, the magnitude of the change being governed by ecological and/or genetic considerations. The following working hypothesis is offered. When food is not limiting, growth is a function of temperature which acts on enzymes. The enzymes have a physiological temperature optimum which may be translated as a physiological temperature optimum for the entire organism. If the growth rates of the several organisms were studied at their physiological optima, their A/B ratios would be about equal.

Furthermore, this transient deviation from the generally accepted logarithmic growth pattern is of great interest to biologists.[2] For example, fishery ecologists working with survival data of larval fish will find that estimates of early survival may be materially altered if a two-phase growth is recognized and used in the computation of survival. The net effect is to raise the estimates of abundance of young larvae and lower the estimates of older larvae, making it possible in some cases to demonstrate an accelerated mortality during the first few days of larval life. This observation may be more readily appreciated after referring to Sette (1943) or Ahlstrom (1954), who developed a method for determining larval survival based on the estimation of abundance of successively older larvae. An estimate of abundance is computed for each of several age groups of larvae. The decline in estimated abundance over the successively older age groups is an estimate of survival. An estimate of abundance of an age group is computed by counting the number of larvae of the age group for the ith sampling station (c_i) and integrating it over the area (w_i) and the time interval (t_i) the sample represents. These several estimates are summed for the year and adjusted for growth to give an estimate of the total abundance (C) of the age groups for the year.

$$\Sigma\, c_i w_i t_i \frac{\text{log rate of growth}}{\text{log range of lengths in size class}} = C$$

[2] Logarithmic growth of larval fishes is discussed by Saville (1956: 14) and Sette (1943: 182).

Since the growth rate affects the estimate of the numbers of fish in a size class, the growth rate would also affect the estimate of survival. A comparison with Ahlstrom's data revealed in this case that the growth suggested by section A for sardines raised the estimates of abundance for these age groups, and the growth rate for section B lowered the estimates of these age groups.

Non-logarithmic growth (when recognized) in larval fish may lead to a more complete understanding of the various factors governing the size of fish populations.

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The Seasonal Development of a Population of *Diaptomus ashlandi* Marsh, and Related Phytoplankton Cycles in Lake Washington

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ABSTRACT

The development of a *Diaptomus ashlandi* population and the simultaneous phytoplankton cycles in Lake Washington, Seattle, were studied in samples taken from October 1949 to October 1950. The lake is 8762 ha in area and 65.2 m deep in its deepest part. Temperature measurements showed that stratification began late in March, and the surface maximum of 22.2° C occurred late in August. Typically the epilimnion was 10 m deep, the thermocline 10 m, and hypolimnion 40 m. Chemical determinations showed the lake to be slightly alkaline usually, but during the summer months the pH was above 8.0. Alkalinity ranged from 0.246 to 0.524 millequivalents/liter. Phosphate determinations showed a winter maximum and summer minimum in the surface and 15 m water, with an accumulation in the bottom waters as summer progressed. Dissolved oxygen was abundant, but in the hypolimnion was depleted at the rate of 2.0 mg/cm²/month during the summer.

Cell volume and chlorophyll measurements showed that a phytoplankton bloom occurred in spring and another in late August. The taxonomic composition of these is presented.

The *Diaptomus ashlandi* population was found to be monocyclic. The period of greatest sexual activity was noted by counting the number of females carrying spermatophores. By this measure transfer of spermatophores lasted for approximately six months starting in January and continuing through July with the peak occurring in April, but egg production occurred from October to the following August, with the largest pulse occurring from mid-January to mid-March. These eggs developed into the nauplius stages which lasted until mid-June. Development through the copepodid stages was traced to October 28 at which time the single annual cycle was complete. Six nauplius and six copepodid stages were noted in the life cycle. The approximate time required for all the nauplii to undergo their development was 75 days. For the copepodids, I and II together required 65 days; III, 40 days; IV, 84 days; V, 90 days; and VI, 5 to 6 months. Study of separate hauls from the epilimnion and hypolimnion showed that the epilimnion was the site of most of the activity of *D. ashlandi* during the period of growth and metamorphosis in the summer.

A coefficient of correlation was computed for chlorophyll concentration and mean number of eggs/sac in the epilimnion. This was 0.598, which was significantly different from zero at the 1 per cent level.

Metasome measurements were made on all the copepodids. These showed that the period of maximal size for the adult females occurred from June to September 1950. This increase in size began just as the peak of phytoplankton had passed. The summer females were found to be significantly larger than the winter females at the 1 per cent level.

Study of the sex ratios showed that females were in excess for much of the year, although males were in excess for as long as 3 months (April, May, June).

INTRODUCTION

The first published record of work done on Lake Washington was an exploratory study make in 1913 by Kemmerer *et al.* (1923). Their work was limited to a single series of chemical and plankton observations. In 1933 Scheffer and Robinson (1939) made a more detailed study of the lake and its biota. They noted the variety in the plankton and time of occurrence of each plankter, but their work was a general study on all the plankton. The present study is concentrated on one zooplankton species as related to the seasonal phytoplankton cycles.

Scheffer and Robinson's work contributed

a considerable amount of information which has been very useful in the evaluation of the results of this study. Their work covered the period from January 1933 to January 1934. They sampled at three stations and found that two phytoplankton pulses occurred, the first during May and the second, which was smaller, in October and November. Their phytoplankton counts were reported as relative frequencies and thus are not quantitative. They noted the similarities between Lake Washington and several of the Great Lakes. With regard to the calanoid populations they noted that *Diaptomus ashlandi* fluctuated with the diatom pulses and gave way to *Epischura* during the summer. The numbers of *D. ashlandi* reached a peak in April and May and diminished to a small population during the last six months of the year. They made no attempt to study the developmental stages of this copepod population and their cyclical fluctuations, but their data on the total population of copepods and phytoplankton have provided a basis for direct comparison with the present study.

We wish to gratefully acknowledge the help of Dr. W. T. Edmondson whose advice on nearly all aspects of this study was generously given. The morphometric data in Table 1 were computed by Dr. Edmondson early in the study; in particular, he stimulated the ideas concerning the significance of cell volume and chlorophyll concentration as measures of the standing crop and potential productivity. Dr. Ruth Patrick of the Philadelphia Academy of Natural Sciences and Dr. R. H. Thompson of the University of Kansas identified the phytoplankters. Jean J. Comita read the manuscript and offered many valuable suggestions. The data discussed were obtained with the aid of the State of Washington Research Fund in Biology and Medicine (Initiative 171).

METHODS

Because only a limited amount of time was available for the field work one station was established from which all samples were taken. Sampling was done from October 29, 1949, to March 14, 1951, although the latter months (Nov. 50 through Mar. 51) were confined to chemical and phytoplankton studies.

Morphometric features were determined from the U.S.C. & G.S. chart number 6449. Contour lines were drawn, and from these contours the area of each of the depth intervals was determined and volumes computed.

Temperature conditions were measured with a bathythermograph, and the Secchi disk was used to determine transparency.

Water was routinely collected with a Kemmerer water sampler at the surface, 15 m, and 55 m for chemical analyses and phytoplankton samples. Chemical analyses included pH (electrometric), dissolved oxygen using the unmodified Winkler method (American Public Health Association 1946), alkalinity titrations with 0.02N sulfuric acid (A.P.H.A. 1946), phosphate (Robinson and Thompson 1948), and chlorophyll determinations (Edmondson and Edmondson 1947).

Phytoplankton samples were prepared by centrifuging 50 ml of lake water in a clinical centrifuge at 1500 rev/min for 10 minutes and preserved in Transeau's solution (water, 95-per cent ethanol, formalin; 6:3:1). Counts were made according to the method described by Lackey (1938), and the length of filamentous forms was estimated by the method of Olson (1950). The volume of each species of phytoplankter was computed by the application of formulae for the volumes of bodies which the species most nearly represented in shape, and from these data the total volume of phytoplankton was calculated.

The Clarke-Bumpus plankton sampler was used for taking the zooplankton samples. It was towed through a considerable horizontal distance while it was being drawn diagonally from the bottom to the top of the stratum being sampled. Two samples of the population were collected on each date, one with a number 10 net, and a second with a number 20 net. The sampling series was begun on the 29th of October 1949, and ended on the 28th of October 1950. All samples were taken between 9 a.m. and noon.

Some of the population estimates were computed from counts of both number 10

and number 20 net samples, but the majority of the estimates were made from single samples only, usually those taken with the number 20 net.

The entire lake was sampled continuously from bottom to top when the lake was homothermal, but during the period of stratification samples were taken separately above and below the thermocline to provide information about copepod distribution.

The counting of the *Diaptomus* population was done on a 3-ml subsample in a small plastic chamber (4 × 4 × ½ cm.) Three such aliquots were counted for each sample and the mean taken. The final estimate of the population was computed from these.

On each date a vertical plankton haul (#25 mesh bolting silk) was made for qualitative enumeration of the organisms in addition to the quantitative hauls. The total number of organisms in this vertical haul was always less than that in the quantitative haul. A Sedgwick-Rafter counting chamber was used for determining the percentage composition in these vertical hauls. From these percentage composition data the ratio of the number of copepodids in the quantitative haul to the number of copepodids in the qualitative vertical haul was found, and this factor was then used to estimate the number of nauplii in the quantitative haul from the number present in the vertical haul. This computed nauplius population was added to the copepodid count to obtain the final total population for the date. This was done because the smaller nauplii were not taken in the number 10 net samples. All copepod populations are expressed as numbers of animals/m^3 (to the nearest whole animal).

PHYSICAL CONDITIONS

Lake Washington is a large (8762 ha), deep (65.2 m), elongate body of freshwater lying in a glacial trough in western Washington (47° 36′ N, 122° 22′ W) (Table 1). In this paper it is not intended to describe the physiography of the region because this has been done by Sheffer and Robinson (1939), and changes subsequent to that time have been published in many papers, some of which are mentioned below. However, it should be mentioned that the lake level is still controlled for shipping operations at the Lake Washington Ship Canal.

TABLE 1. *Morphometric data for Lake Washington*

Measurements are taken from U. S. C. & G. S. chart number 6449.

Depth m	Area ha	Volume 10^6 m^3	% total volume
0	8,762		
		420.6	14.58
5	8,076		
		383.9	13.31
10	7,292		
		350.8	12.16
15	6,746		
		322.4	11.18
20	6,158		
		294.6	10.22
25	5,636		
		267.3	9.27
30	5,066		
		230.3	7.98
35	4,164		
		190.7	6.61
40	3,477		
		156.6	5.43
45	2,802		
		121.3	4.20
50	2,069		
		91.5	3.17
55	1,602		
		46.9	1.63
60	406		
		7.7	0.25
65	2		
		0.001	0.00004
65.2	0		

Total volume 2,884.2 x 10^6 m^3
Mean depth 32.9 m

Autumn mixing of the lake began early in November 1949, and full circulation at 8.0° C was attained by December (Fig. 1). The minimum temperature was recorded in February 1950 when the lake was homothermal at 4.6° C. Stratification began in late March, and the maximum surface temperature of 22.2° C occurred in late August. Typically the lake had an epilimnion of 10 m, a thermocline of 10 m, and a hypolimnion of 40 m. Full circulation again became evident in December 1950 when the temperature was slightly above 9.0° C. The relatively high bottom temperature recorded during September and October was due to the intrusion of salt water from the

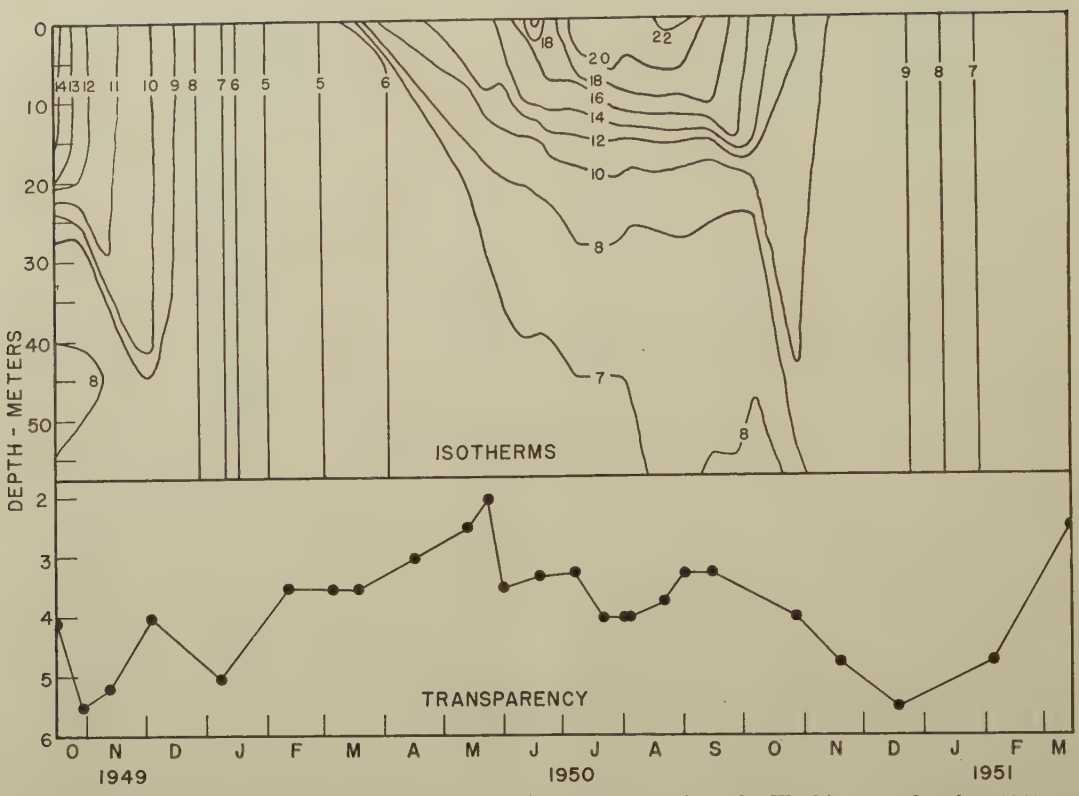

FIG. 1. Seasonal variations of temperature and transparency in Lake Washington, October 1949 to March 1951.

Lake Washington Ship Canal, but there has not been a sufficient amount added in any year to interfere with complete winter circulation (Seckel and Rattray 1953). The annual heat budget in 1950 was 26,452 g-cal/cm^2; this contrasted with a value of 23,655 in 1933.[1]

Transparency was generally low in summer and high in winter, ranging between 1.8 m in May and 5.5 m in December 1950 and October 1949 (Fig. 1). The arithmetic mean for the period studied was 3.82 m.

CHEMICAL CONDITIONS

Seasonal and vertical variations of the chemical determinations made are shown in Figure 2. The lake was generally near neutrality or slightly alkaline; the fluctuations in pH were small except during June, July, and August. During these months the pH was consistently above 8.0 which was apparently due to removal of CO_2 by photosynthesis with a resultant rise in pH. Alkalinity, represented only by bicarbonate, remained in the range 0.246 to 0.524 milleequivalents/liter. At most times the bicarbonate was nearly equal at all depths, and there was no observable hypolimnetic accumulation as summer stratification progressed. With the present data it is not possible to explain the large increase which occurred at all depths during March 1950. Part of the increase is probably related to inflow which reached a seasonal maximum early in March. However, the major tributary, Cedar River, had a bicarbonate concentration of only 0.420 me/L. Reexamination of the original data revealed no errors in calculation or faulty standard solutions.

The phosphate concentration of the entire

[1] Scheffer and Robinson (1939) reported an erroneous value of 43000 g-cal/cm^2 in 1933 which apparently was due to use of the maximum depth rather than the mean depth. Their reported mean depth of 18 m is actually that depth at which half of the total volume of the lake is above or below the level.

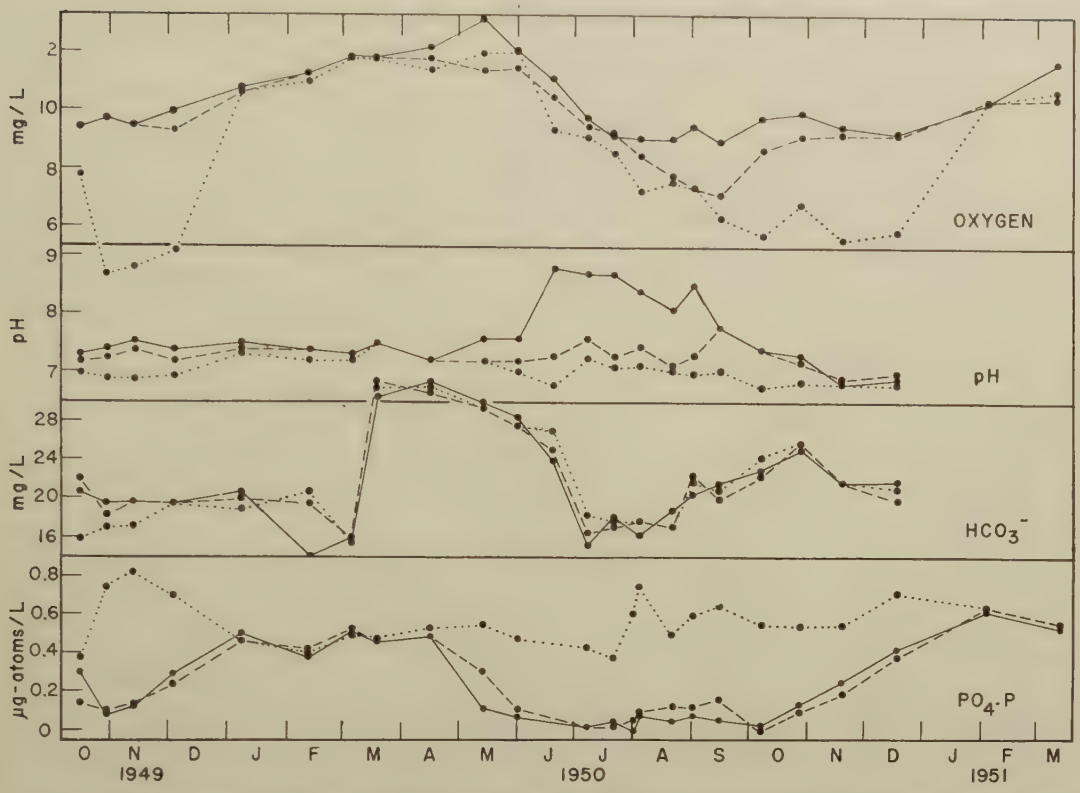

FIG. 2. Seasonal and vertical variations of dissolved oxygen, pH, alkalinity, and phosphate in Lake Washington, October 1949 to March 1951. The solid line represents concentration at the surface, dashed line at 15 m, dotted line at 55 m.

lake remained near 0.5 µg-atoms/liter during the period of complete mixing in winter. At the beginning of spring, with the onset of thermal stratification and the growth of the phytoplankton, phosphate in the epilimnion gradually decreased to between 0 and 0.1 µg-atoms/liter, where it remained until autumn mixing began in late October. In the bottom waters during the course of the summer there was a gradual but erratic accumulation of phosphate due to the settling of organic matter from the surface waters and its subsequent decomposition. The phosphate once again became equally distributed in the lake after winter circulation was established.

Dissolved oxygen was generally abundant. At the beginning of thermal stratification, and the consequent increase in growth and photosynthesis of the phytoplankton, the surface waters increased in oxygen content, reaching a maximum of 13.2 mg/liter on May 13. During the course of the summer there was a gradual decrease in oxygen content in the hypolimnion (minimum 5.6 mg/liter at 55 m) due to the decomposition of organic material derived from the epilimnion. Oxygen concentration was evenly distributed during periods of winter circulation.

Hypolimnetic oxygen deficits (Hutchinson 1938) have been calculated for 1933 1950, and subsequent years. There appears to have been an increase in deficit with time, *i.e.*, 1.18 mg/cm²/month in 1933 and 2.00 in 1950. This increase has been related to increasing amounts of sewage and possibly other nutrient-rich drainage added to the lake in recent years, the significance of which has been discussed in an earlier paper (Edmondson *et al.* 1956). Also a fairly close relation between oxygen decrease and phosphate increase in the hypolimnion has been noted.

TABLE 2. *Weighted mean seasonal variations in cell volume of Lake Washington phytoplankters*
Each entry multiplied by 10^3 will give μ^3/ml. Epilimnion only.

	Average vol/cell	Feb 11	Mar 5	Apr 15	May 13	June 24	July 21	Aug 4	Aug 21	Sept 1	Sept 15	Oct 28	Nov 19	Dec 18	Feb 4 (1951)	Mar 14
CHLOROPHYTA		46.4	67.4	61.3	118.7	69.6	3.7	21.2	7.3	51.3	64.7	5.7	3.2	22.1	66.9	
Ankistrodesmus falcatus	0.6					1.0	0.6				0.6	5.7	3.2	0.6	2.4	
Coelastrum microporum	1.6		42.3		37.3											
Cosmarium sp.	5.9	11.1	6.3	31.9	67.0									6.3		
Crucigenia rectangularis	0.5										14.7					
Dictyosphaerium ehrenbergii	1.9	0.2														
Oocystis borgei	1.9			16.1												
Oocystis parva	0.3	9.5	1.3	13.3	14.4	8.0	3.1	1.0	7.3							
Sphaerocystis schroeteri	1.9	25.6	17.5					19.6								
Staurastrum paradoxum	5.9					9.3										
Staurastrum pseudopelagicum	32.3					51.3				51.3	49.4			15.2	64.5	
CHRYSOPHYTA		528.2	266.0	2133.0	942.9	485.6	157.0	46.9	26.6	172.8	209.1	64.2	137.8	179.6	155.9	44.8
Botryococcus braunii	**	8.3			18.6	3.3	18.6									
Dinobryon borgei	0.1	0.3		0.3					4.2	0.3						
Mallomonas producta	2.7								5.8							
Asterionella formosa	0.6	6.0	8.5	1.3	32.5	2.9	0.6		0.6	13.9	0.3			2.3	2.5	1.2
Cyclotella bodanica	8.3		71.6	464.2	332.0	210.0	43.1	20.6		13.2	130.4		15.7	8.9		
Cyclotella ocellata	0.3			9.5	1.3	1.0	0.8				0.1					
Fragilaria capucina	0.1				0.4	0.2										
Fragilaria crotonensis	0.3		1.1	14.0	86.2	215.0	65.4	0.5		3.2	19.7	2.9	0.7	2.2	9.7	1.3
Melosira italica	0.8	147.0	142.7	58.8	16.7			0.9			3.1	4.4	4.3	10.9	38.4	9.2
M. italica var. tenuissima	0.2	0.3	3.4	7.1	1.0											
Melosira varians	1.0	349.6	14.6	44.5	69.4	7.2	6.3	14.5		3.4	8.6		39.0	10.9	74.8	18.4
Rhizosolenia gracilis	2.3		11.3	15.2	195.6	9.1	3.7	3.2		21.9	10.9	29.5	53.2	12.8	13.8	4.6
Stephanodiscus astraea	1.2	2.5		10.4	13.3	14.3	9.9	5.6	1.2	3.0	9.9	8.3	12.0	1.8	4.7	
Stephanodiscus niagarae	117.9			1497.4	125.0					110.8				125.0		
Synedra acus	0.9	1.8			8.0	6.5	0.8				9.8	13.6	4.4	0.4		
Tabellaria fenestrata	4.2								13.5		4.5					
Miscellaneous diatoms	0.6	12.4	12.8	10.3	42.9	16.1	7.8	1.6	1.3	3.1	11.8	5.5	8.5	4.4	12.0	10.1
PYRROPHYTA				226.5		100.4		50.6	1997.5	169.8						
Ceratium hirundinella	106.8			226.5		100.4				169.8						
Peridinium divergens	47.7							50.6	1997.5							

TABLE 2.—(*Continued*)

CYANOPHYTA		326.9	114.6	135.8	72.7	23.3	35.9	30.0	3.4	30.1	331.6	32.1	28.1	7.0	6.2	27.4
Anabaena circinalis	0.2									4.8	1.4					
Anabaena sp.	0.04							1.2			9.3	7.2	4.0	0.1		
Aphanizomenon flos-aquae	0.06				1.4											
Aphanocapsa delicatissima	**			4.8	2.2			15.3		12.9	108.4					
Aulosira sp.	0.2										47.1	4.0				
Coelosphaerium Naegelianum	**						17.2	7.7			14.3				4.1	
Gomphosphaeria lacustris	**	7.8									7.3					
Microcystis aeruginosa	**										7.3					
M. aeruginosa var. major	**					8.7					83.1					
Oscillatoria agardhii	0.3*	317.0	114.1	128.3	68.1	11.0	15.7	3.2	3.4	5.0	2.4		1.7	0.6		26.2
Phormidium sp.	0.02*	2.1	0.5	2.7	1.0	3.6	3.0	2.6		7.4	58.3	20.9	22.4	6.3	2.1	1.2
MISCELLANEOUS	0.2	5.7	0.3	0.8	4.4	0.9	0.3	0.2	1.3	0.7	1.8	0.3	0.2	1.3	0.4	
TOTAL		907.2	448.3	2557.4	1138.7	679.8	196.9	148.9	2036.1	424.7	607.2	102.3	169.3	210.0	229.4	72.2

* volume of a filament 24.3 μ in length
** volume of ach colony measured individually

PHYTOPLANKTON

Thirty-six genera, 49 species, and two miscellaneous groups made up the phytoplankton. One miscellaneous group was composed of diatoms, the other of unrecognizable forms of green and blue-green algae. Scheffer and Robinson (1939) reported 49 genera and 72 species, the difference being mainly due to a decrease in variety of green algae in 1950. The following discussion of the phytoplankton population is confined to those forms found in the 0 to 15 m zone, because forms found beneath this depth probably represent dead or dying cells in the process of settling to the bottom (Table 2).

Cell volume and chlorophyll concentration are used to show the seasonal variations of phytoplankton. As there is some variation between the two indices it seems advisable at this time to discuss the significance of each.

For purposes of the present study, cell volume is probably a better measure of the standing crop of phytoplankton than chlorophyll in view of the different chlorophyll concentrations per unit of cell material found between different species of algae and within a given species under different physiological conditions. Also, chlorophyll in dead and dying cells and fecal pellets of animals is measured along with chlorophyll in viable phytoplankton material. However, in terms of potential productivity of the population, chlorophyll is probably a better index as has been demonstrated in laboratory (Fleischer 1935, Emerson *et al.* 1940) and natural populations (Gessner 1949, Edmondson 1955, Ryther and Yentsch 1957). In the above cited works, it has been shown that the ability to photosynthesize varies with the amount of chlorophyll, other factors being held constant. In the present paper both measurements are used—cell volume to designate the phytoplankton biomass present at any time, and chlorophyll concentration as a measure of the potential reproductive capacity as well as a measure of the physiological condition of the population.

In Lake Washington cell volume and chlorophyll concentration showed generally parallel seasonal trends, except during the spring bloom when the maximum volume of phytoplankton, occurred in mid-April and the chlorophyll maximum was found in the latter part of May (Fig. 3). With the beginning of thermal stratification the spring bloom was initiated. During this bloom there was a steady increase in oxygen but no immediate change in pH; later a drop in the phosphate and transparency followed

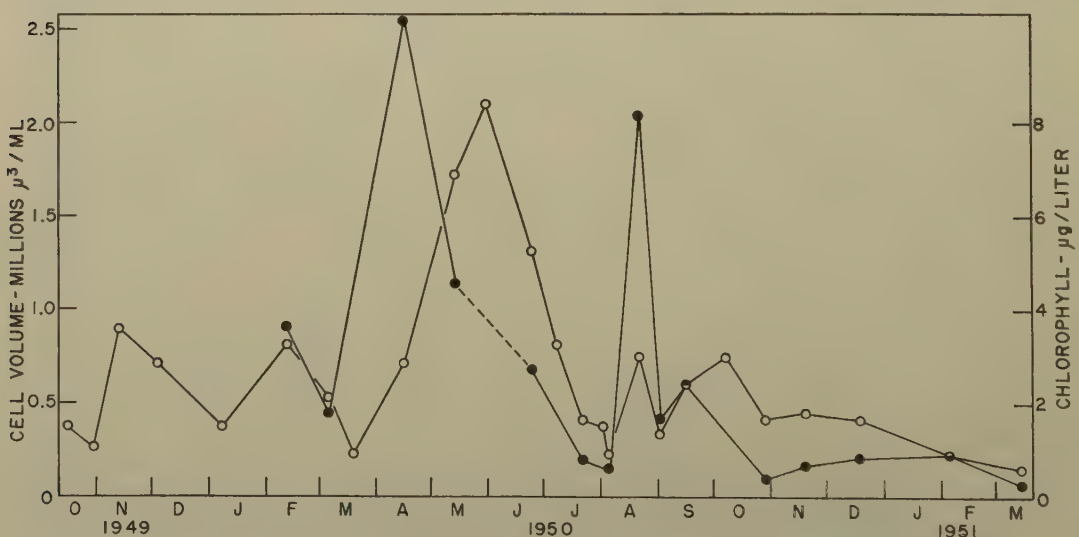

FIG. 3. Seasonal variations of phytoplankton volume (closed circles) and chlorophyll concentration (open circles) in the 0–15 m zone in Lake Washington, October 1949 to March 1951. Weighted averages.

by a marked increase in pH in the epilimnion occurred. The spring bloom was essentially over by the end of June, and a midsummer minimum persisted until late in August. Evidently conditions once again became favorable for growth in the latter part of August as a second annual bloom of short duration composed almost entirely of *Peridinium* was produced. There was a further slight increase in the population in the middle of September and then a decrease and leveling off of the population through the winter.

Some explanation for the low chlorophyll concentration per unit of cell material in April as contrasted with that recorded in May may be found in the qualitative makeup of the population throughout this period. *Stephanodiscus niagarae*, a large diatom with little chlorophyll per unit of cell material as judged by visual observation, contributed more than one-half of the total phytoplankton population in April but had considerably diminished by May. This, in effect, was largely responsible for the discrepancy noted in the spring between the chlorophyll concentration and the cell volume.

The Chrysophyta, which almost entirely made up the spring bloom, retained its dominant position until August when the Pyrrophyta became dominant and almost exclusively made up the second bloom. The short Pyrrophyta bloom was followed in mid-September by a small pulse of Cyanophyta. The Chrysophyta became dominant once again in late fall and remained that way throughout the winter.

The diatoms were represented by a large number of species, 16 in all. *Melosira varians* and *M. italica* both showed spring blooms and were present at most times of the year. *M. italica* var. *tenuissima* formed a small pulse in the spring. *Stephanodiscus niagarae* was present only for a short time in the spring and in relatively small numbers, but due to its large size it was the dominant species. It was observed again in the fall and in winter in small amount. *Fragilaria* was present at most times and formed a pulse in the latter part of June and in the fall, as did *Rhizosolenia*. *Asterionella* and *Synedra*, both common forms in occurrence but inconspicuous in amount, showed both spring and fall increases. *Cyclotella bodanica*, one of the dominants, was abundant from March through July and showed another lesser pulse in September.

Presumably, silicate conditions in Lake Washington are favorable much of the time for the growth of the diatoms. Scheffer and Robinson (1939) measured the seasonal distribution of silicate in 1933 and 1934. During both winters of their study the surface concentration remained near 3.0 mg/liter, while in April, 1933 there was a gradual decline to a minimum of 0.8 mg/liter at the end of May. There was then a gradual increase to approximately 2.0 mg/liter by September followed by another slight decrease and an increase until winter conditions were again restored. The diatom population in 1933 varied inversely with the silicate cycle, as did the 1950 diatom population with the 1933 silicate data. Although the silicate level was not reported to have decreased below the critical level of 0.5 mg/liter for continued diatom growth (Pearsall 1932, Lund 1950), it was sufficiently low to suspect that it might have been limiting. It is possible that it did reach or drop below the critical level between measurements during the spring minimum.

The Chrysophyceae were represented by only two species that were noted in late August, *Mallomonas producta* and *Dinobryon borgei*, both of which were relatively unimportant.

The Pyrrophyta were represented by two species, *Ceratium hirundinella* and *Peridinium divergens*. In spite of the small number of species, the Pyrrophyta were second in total abundance in the lake and were the dominant group in late summer. This dominance was mainly due to *Peridinium* which amounted to 1,997,500 μ^3/ml on August 21. On the next sampling date, September 1, *Peridinium* was absent but *Ceratium* was the dominant form. After this time the group disappeared altogether.

The Cyanophyta were represented by 11 species, but these made a relatively inconspicuous contribution to the volume. *Oscillatoria* and *Phormidium* were present almost continuously. *Oscillatoria* was in greatest abundance and one of the dominants in

late winter, whereas *Phormidium* occurred in greatest quantity in mid-September. *Anabaena*, *Phormidium*, *Coelosphaerium*, *Aphanocapsa*, and *Microcystis* made up a small but dominant blue-green pulse in mid-September.

The Chlorophyta as a group did not become dominant at any time, nor did any of its members. *Oocystis parva*, *Cosmarium*, and *Coelastrum* were reasonably abundant in the spring. *Staurastrum pseudopelagicum*, *Crucigenia*, and *Ankistrodesmus* were common in the fall.

THE DIAPTOMUS POPULATION AND THE PHYTOPLANKTON CYCLES

There were several species of copepods in the plankton during 1940–1950. These were *Diaptomus ashlandi* Marsh, *Epischura nevadensis* Lilljeborg, and *Cyclops bicuspidatus thomasi* S. A. Forbes, the same species reported by Scheffer and Robinson (1939). Of these species only the *Diaptomus* population was studied.

The development of *Diaptomus ashlandi* was monocyclic, requiring the entire year for completion. Scheffer and Robinson (1939) noted that *D. ashlandi* was common in winter, increasing in abundance from February to a peak in April–May and almost disappearing by July. They stated that a much smaller pulse occurred in October. From their information and the present data it appears that the life cycle of *D. ashlandi* follows essentially the same seasonal periodicity from year to year, except that it can be displaced to some earlier or later period of time. This displacement in time probably depends upon environmental influences such as temperature, amount of food, etc. In 1933 the peak population occurred earlier than it did in 1950, but the abrupt disappearance of the majority of the immature stages occurred about the same time for the two years.

From the appearance of the pulses of all the developmental stages in the life history (Fig. 4) the life cycle was worked out. The long period of egg production is reflected in the prolonged existence of each of the larval stages through the year. The eggs from which these larvae emerged were produced at a time when the lake was homothermal,

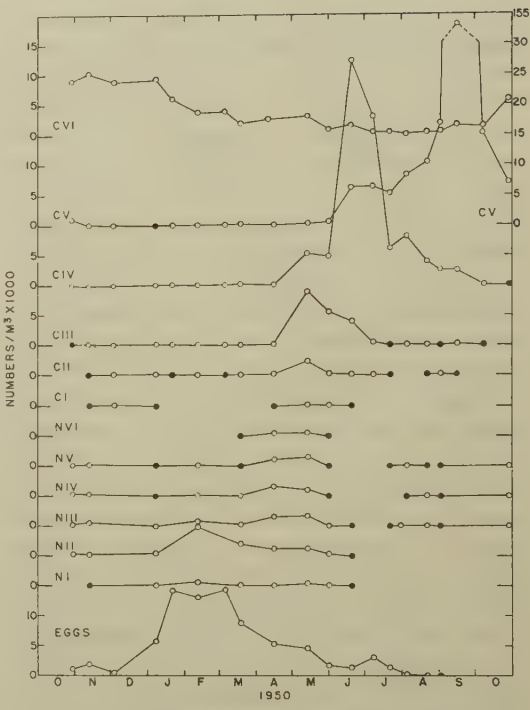

FIG. 4. The population numbers of the developmental stages of *D. ashlandi*. *C* = copepodid, *N* = nauplius, eggs = total eggs. Scale for stage V copepodids on left and right ordinate but right ordinate is complete. Uppermost graduation on right ordinate represents 125 units. Open circles represent dates on which a population count was made. Closed circles represent dates of zero population. Data plotted are corrected for lake volume.

temperature conditions were minimal, and the algal population was very low. Figure 3 shows a small chlorophyll pulse in the 0–15 m zone in mid-November 1949. This pulse was followed by the period of high egg production (Fig. 4). A second, large pulse of algae did not occur until well after egg production declined. This second pulse of algae was maximal for 1950, and developed while the last nauplii were still present and the early copepodids were abundant.

The time required for the development of each of the nauplius stages could not be obtained from these data, because the date of their peak occurrence was not distinct.

The time of molting of the copepodids from Stage I to II to III is also not clear, but from the curves presented in Figure 5 the concurrence of the peaks of each of those

stages indicates that the two stages are passed within a period of less than eight weeks. Although only four samples were taken during this time, the counts show that the peak of copepodid stage IV is displaced sufficiently to indicate that the time interval spent in stage III was roughly about 40 days. This was derived by noting that the peak of stage III occurred about May 20 and that the peak of stage IV occurred just before July 1.

The peak for stage V may possibly have occurred about September 15, but this seemed to be an unreasonably high peak as estimated from the counts of the samples for this date. Four samples were taken on this date, and the population estimates from all of them were extremely high. All of these samples were of a low number of revolutions on the sampler counter indicating that the sampler was not operating properly. The mean population computed from these samples is shown, but its magnitude is much reduced in the figure. Since there was a steady increase in the stage V population up to this date, the placement in time of this peak was accepted as being nearly correct. If this is true, the time interval for stage IV would be about 84 days (from June 28 to September 15).

An estimation of the longevity of stage VI is impossible from this series of data since sampling stopped at the end of October. Nonetheless, conditions at the end of the study were similar to those at the beginning so that the cycles met with some degree of compatibility. On the assumption that the cycles were very similar, it appears that the adult population may have reached a peak at or near December 1, so that stage V copepodid instar may possibly have existed about three months. The adults that were produced from these V's then produced the eggs of the new generation in the early months of the following year. The cycle thus corresponded closely with the calendar year. The estimates of the longevity of each of the copepodid instars are listed in Table 3.

When comparing the number of days required for development by each of the copepodid instars (III, 40 days; IV, 84 days; V, 90 days) it was noticed that the time required for development of stage IV is disproportionately long. This increase in time occurred when the chlorophyll and cell volume dropped to the very low level noted late in July. This may be the cause of the increase in time required for development of the stage IV copepodids.

The data presented here show that *Diaptomus ashlandi* has only one distinct breeding period in a year as contrasted with *Calanus finmarchicus* which has several (Nicholls 1933). During 1950 there was one long prominent period of egg production at the beginning of the year which had diminished considerably by the end of May but did not disappear completely until the end of August. This low point in egg production that is noted in June may possibly be a reflection of the simultaneous sharp drop in cell volume and chlorophyll which began in June and reached a minimum in early August. It appears probable that this sharp drop in phytoplankton resulted in starvation of even those few nauplii that hatched during this time, because for much of June and all of July there were no nauplii and few copepodids up to stage III.

No attempt was made to study vertical migration of this copepod; however, study of the split hauls showed that the population was concentrated in the epilimnion on nearly every date that hauls were taken. Table 4 shows that during times of stratification for copepodids IV, V, and VI, there were more animals in the epilimnion (exceptions

TABLE 3. *Approximate duration of stages of D. ashlandi*

Duration represents the approximate number of days the stage was noted in the samples. The temperature range of the lake in the epilimnion and hypolimnion is also presented.

Stage	Duration	Temperature range, °C			
		Epilimnion		Hypolimnion	
		Min.	Max.	Min.	Max.
All nauplii	75 days	4.5	13	4.5	7.5
Copepodids:					
Stages I and II	65 days	9	15.5	6	7.5
Stage III	40 days	9	15.5	6	7.5
Stage IV	84 days	13	21	7.5	8
Stage V	90 days	12	21	7.5	8
Stage VI	5 to 6 months (?)	4.5	17	4.5	8

TABLE 4. *Sex ratios of Diaptomus ashlandi in 1949 and 1950*

Ratios are given as females/males. Where the word males or females appears in the ratio column, the catch was entirely of that sex; therefore, the catch for that particular day did not enter into the computation of the mean for the year. *E*, *H*, and *T* denote epilimnion, hypolimnion, and total, respectively, and indicate the population and ratio computed from specimens taken from that stratum or for the entire water column sampled (*T*) when the lake was not stratified. Population data are numbers/m³ and are uncorrected for lake volume. Asterisks indicate days on which the epilimnion had fewer animals than the hypolimnion.

Date		Copepodid Stages					
		IV		V		VI (Adults)	
		Population	Ratio	Population	Ratio	Population	Ratio
1949							
29 Oct.	E	30	females	1876	0.13	13241	0.77
	H	0	—	370	0.13	5106	1.39
12 Nov.	E	16	males	66	males	12616	0.84
	H	0	—	26	females	7433	0.90
3 Dec.	E	74	2.5	11*	males	8298	0.75
	H	14	males	28	males	6937	0.93
1950							
7 Jan.	T	122	7.1	0	—	9351	0.72
21 Jan.	T	64	1.0	32	1.00	6101	0.73
11 Feb.	T	54	0.74	69	2.00	3872	0.96
5 Mar.	T	94	0.34	68	3.00	4038	1.14
18 Mar.	T	286	1.0	180	0.26	2037	1.05
15 Apr.	T	119	0.51	63	0.58	2694	0.88
13 May	E	31590	0.71	2067	6.44	18366	0.25
	H	538	0.44	5	females	459	0.91
31 May	E	7465	8.51	1231	1.70	1297	0.25
	H	3122	0.99	240	14.00	787	0.73
19 Jun.	E	90800	0.72	14550	3.42	3329	0.63
	H	1385	0.67	1399	1.81	716	0.53
7 Jul.	E	33300	0.96	5220*	2.41	630	1.33
	H	26190	0.87	7407	3.17	463	5.01
21 Jul.	E	15895	1.01	10505	2.46	299*	females
	H	2313	1.12	3302	1.74	554	2.67
4 Aug.	E	12390	0.50	13880	1.90	249	females
	H	3801	0.89	2778	19.13	33	1.2
21 Aug.	E	5622	0.62	12670	0.85	452	5.46
	H	1568	0.35	7345	1.83	406	3.10
1 Sept.	E	2100*	0.25	23210	0.81	467*	8.94
	H	3647	0.013	7165	1.36	501	15.16
15 Sept.	E	4854	0.44	205450	0.85	2240	females
	H	61	males	12210	1.12	939	8.21
7 Oct.	E	122	0.42	24930	0.88	1375	4.33
	H	0	—	8575	0.87	1360	6.66
28 Oct.	T	0	—	7070	0.28	5929	1.78
Mean ratio for the year			1.31		2.74		2 61

designated by asterisks) than in the hypolimnion. On May 13, when stratification was definite, there was a marked concentration of all stages in the epilimnion; this concentration was 25 to 300 times that in the hypolimnion. At this time the surface water contained the greatest concentration of chlorophyll as compared to that of the rest of the year. On the following sampling date, May 31, the number of copepodids in the epilimnion had dropped considerably; only stage III copepodids showed a continued strong concentration in the epilimnion. On June 19 the greatest number were of stage IV copepodids, both males and females, which were nearly all in the epilimnion. Following June 19 there was a concentration of copepodids IV and V in the epilimnion,

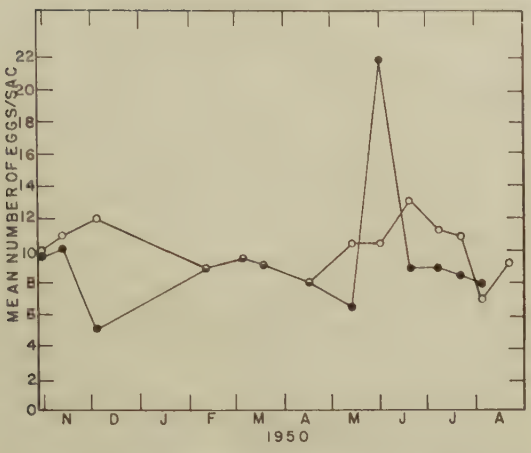

FIG. 5. Variation in the mean number of eggs per sac. Closed circles represent egg counts from epilimnetic females. Open circles are from hypolimnetic females. Circles half open are from females during unstratified times.

but it was less than was noted previously. Until September 1 as the depth of the epilimnion increased the animals were still largely in the epilimnion, but the hypolimnion showed greater numbers than before. On September 1 in the epilimnion, which was approximately 61 % of the lake volume, a concentration of copepodid V's was noted. These copepodids remained concentrated in the epilimnion until the lake turned over late in October. Thus the concentration of *D. ashlandi* in the epilimnion through the entire time of stratification indicates that it is possible for most of the copepodids to undergo their entire development in that layer. The strong drop in the epilimnetic chlorophyll after the month of June is interpreted as being additional support for this.

It is possible that the time of highest chlorophyll concentrations and mean number of eggs/sac in *D. ashlandi* may be causally related (Fig. 5). The number of eggs/sac in the epilimnion increased from a mean of about 5 on December 3, 1949; to a mean of 32 on May 31. A chlorophyll peak was noted at approximately the same time but lagging by about one sampling date. A somewhat similar time lag was noted in the hypolimnion. The coefficient of correlation for these two events after advancing the chlorophyll data one date was 0.598, which is significantly different from zero at the 1 per cent level. It is probable that the food consumption increased during times of high chlorophyll, and as a consequence more eggs were formed in the sacs. However, it was not during the periods of high chlorophyll that the heavy pulse of eggs occurred, but mainly during a period of low chlorophyll. During the period of heavy egg production in the latter part of January, the entire month of February, and most of March, between 8 and 17 per cent of the females were ovigerous in the samples. About mid-March 37.4 per cent were ovigerous, and through mid-May the percentage decreased to about 25. This percentage then gradually declined to zero by mid-August.

A study was made of the number of eggs produced by epilimnetic and hypolimnetic ovigerous females (Fig. 5). On all but two dates on which split hauls were taken the ovigerous females in the hypolimnion carried a greater mean number of eggs/sac. This might suggest that females which produce the larger number of eggs/sac may be drawn into the hypolimnion as a consequence of this additional weight. Also through June and July 1950 (as well as in November 1949), large ovigerous females were found consistently in the hypolimnion (Fig. 6).

The size of the animals was investigated by measuring the length of the metasome on 25 or more individuals on each date (Fig. 6). These measurements show a period of maximal size for the adult females which occurred during June, July, August, and September. The mean length[2] of the adult females was 0.91 mm for the warm period, June through September. For the colder period, October through May, the mean length was 0.81 mm. By the *t* test the "summer" female was found to be significantly longer than the "winter" female at the 1 per cent level. In the adult males the length measurements varied as did those of the adult females and at approximately

[2] In Figure 6 median lengths were plotted, but for the comparison of the lengths during the warm and cold periods mentioned the mean lengths were used. For these measurements the two are nearly identical.

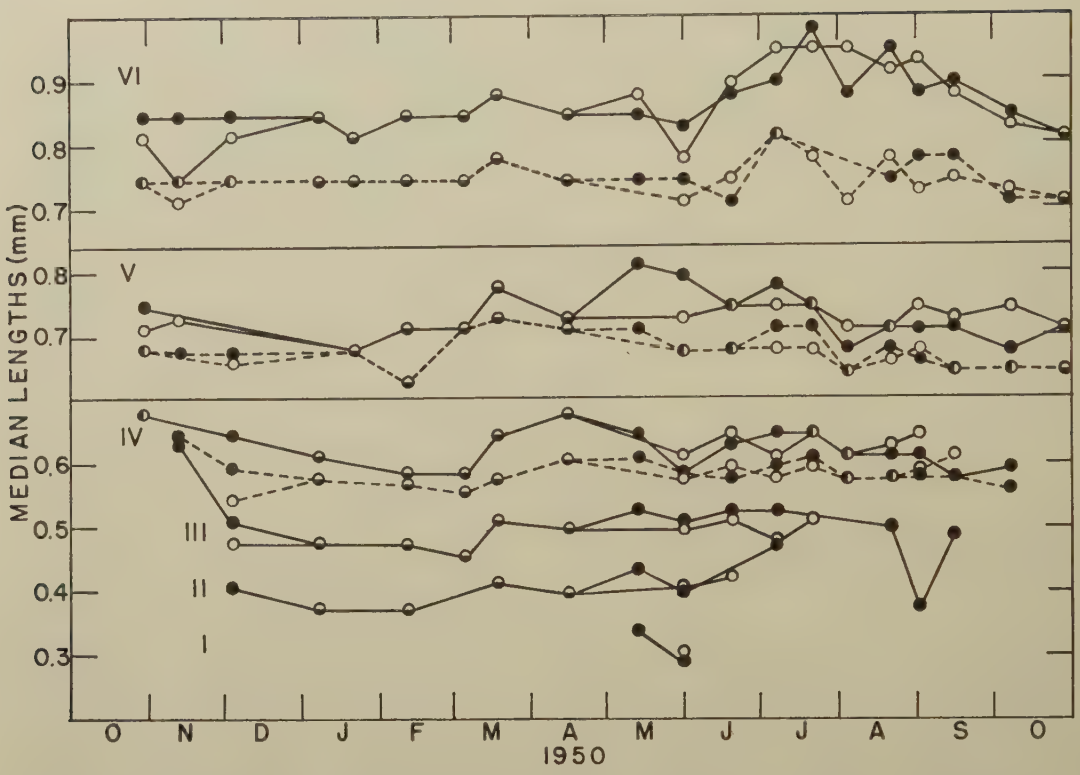

FIG. 6. Median lengths of the metasome of the copepodid stages of *D. ashlandi*. Solid lines are for females; dashed lines are for males. Closed circles are measurements of specimens taken from the epilimnion, open circles, the hypolimnion; circles half open are taken from specimens throughout the water column. Stages I, II, III are represented by two lines, one epilimnetic and one hypolimnetic. Stages IV, V, and VI are represented by four lines when the lake was stratified: two are for epilimnetic and hypolimnetic females and two are for epilimnetic and hypolimnetic males.

the same time, but the fluctuations were smaller. The length measurements for stage V copepodids showed an increase in size in both the males and females. There was a period of fluctuation just as there was in the adult males during the period of greatest increase in size shown by the adult females. Stage IV copepodids showed the same length fluctuations as did the V's, the fluctuations being of smaller magnitude but occurring in the same time interval. The statistical significance of these deviations was not investigated. The fluctuation of stages II and III were of even smaller magnitude, and only a few measurements were obtained for stage I. For the copepodids that show sexual dimorphism (IV, V, and VI), the females were longer than the males throughout the year.

Coker (1933) found that temperature had a direct effect upon size of copepods, those reared in cold being larger than those reared in warm water, and that lack of food delayed development but had no direct effect on size. These data appear to support Coker's temperature relationships but are not conclusive. The large females of June, July, August, and September were preceded by large stage V copepodids (possibly March and April, certainly May and early June, and possibly July) and these in turn by larger size stage IV copepodids (March, April, and May). These larger animals are traceable more or less as a pulse through these three instars. If this follows, the animals of this pulse were reared from the egg crop of January, February, and March, and their early development must have taken place under cold temperatures and while an abundant

supply of food was present. Estimates of the times required for development of this larger group of animals indicate they required less time for development than that required for each of the instars when all of the animals were included. Stage IV required about 30 days (estimated from data in Fig. 6) as compared with 84 (estimated from data in Fig. 4), and stage V 70 days as compared with 90. These data appear to support Coker's results in that the abundance of food may have increased the rate of development of this group of animals, and the colder temperatures during their development resulted in their larger size. However, it is impossible to separate the effect of temperature and amount of food available for this population, because those animals reared during the colder temperatures had an abundance of food and those reared during the warmer temperatures had a scarcity of food. These data also agree with the data taken on *Limnocalanus* (Comita 1956) for which it appeared that food supply controlled the size.

The first stage wherein sex is apparent is stage IV. Examination of the sex ratios (Table 4) shows that there was no numerical predominance of one sex over the other from October 1949 through January 1950 in this instar. For the remainder of the time there were generally more stage IV male copepodids than female. In stage V the females were in excess for most of the year, whereas in the adults more commonly the males were in excess from October 1949 through June 1950. However, the mean for the year shows that there are more females for all three instars. For *Calanus*, Marshall *et al.* (1934 and 1955) found that the proportion of males to females caught is low and varies from place to place. In *Limnocalanus johanseni* there was noted a slight excess of males in the C V's but slightly more females than males in the adult stage (Comita 1956).

It should be noted that the excess of males occurred during much of the period of sexual activity, which was determined by counting the number of females carrying spermatophores (Table 5). These counts showed that this period was the first six months of the year with a peak occurring about April 1. This is coincident with the earliest part of the algal bloom. However this is not coincident with the egg peak shown in Figure 4, which occurred at approximately mid-February. Examination of the sex ratios shows that males were more or less abundant in the last three instars during November and December and up to middle February in the adult stage. Also in the adults during March the ratio approached very closely to one, but males were in excess during April, May, and June. Since more males than females were present after 18 March an excess of spermatophores may possibly explain why there was a peak of females carrying spermatophores occurring around the 1st of April, whereas the peak of eggs occurred around the middle of February. It is possible that most of the eggs had been fertilized before the peak of occurrence of females bearing spermatophores, and that spermatophore attachment continued at an increasing rate because of the excess of males.

Following the ovigerous period the adults apparently died off, but they were never absent. On August 4 there were as few as 143/m^3, and there was an excess of adult

TABLE 5. *Per cent females bearing spermatophores, Diaptomus ashlandi, in 1949 and 1950*

Counts were made of the number of females noted to carry one or more spermatophores, and these are expressed as a per cent of the entire female population for that date.

Date	Per cent
1949	
3 Dec.	0
1950	
7 Jan.	25.0
21 Jan.	17.6
11 Feb.	38.6
6 Mar.	22.6
18 Mar.	39.6
15 Apr.	48.0
13 May	27.5
31 May	35.0
19 Jun.	28.6
7 Jul.	0
21 Jul.	4.4
4 Aug.	0

females over males for the remainder of the time.

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The Effect of Various Factors on the Toxicity of Sodium Pentachlorophenate to Fish[1]

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ABSTRACT

The effects of various factors on the toxicity of sodium pentachlorophenate to the fathead minnow (*Pimephales promelas*) were studied. As a base for comparison of the effects of various factors, the TL_m for 24 hours was first investigated. It was found that 0.4 ppm killed all the fish, while they all lived at 0.20 ppm. The range between these two extremes was so slight that it was difficult to determine an exact 24-hour TL_m; it was found to lie between 0.32 and 0.35 ppm.

One ppm concentration of sodium pentachlorophenate was used for investigating the effect of pH on the toxicant at 18° C. It was found that the lower the pH of the test solution, the more toxic the material became. The mean survival time for 50% of the experimental animals at a pH of 5.9–6.0 was 28 ± 1.7 minutes; at 7.5–7.6, it was 80.7 ± 2.3 minutes; and at 8.9–9.0, the fish lived for 24 hours.

Temperature effects were investigated using a solution of one ppm of sodium pentachlorophenate at pH 7.5–7.6. It was found that the higher the temperature, the more toxic the sodium pentachlorophenate is to fish.

The mean survival time of 50% of the minnows at 10° C was 260.4 ± 10.2 minutes; at 18° it was 80.7 ± 2.3 minutes; and at 26° it was 46 ± 2.1 minutes.

INTRODUCTION

With industrialization the waters of our streams and rivers are receiving an increasing load of industrial wastes. Besides polluting the waters, in many cases these wastes kill fish and other aquatic organisms. A number of studies have been made to obtain precise information on the toxicity of various industrial wastes to fish (Ellis 1937, Doudoroff and Katz 1950 and 1953, Doudoroff *et al.* 1953, and Trama 1955). These and other studies include investigations on most common pollutants, both singly and in combination.

All these studies are very valuable and have provided much needed information. In only a few cases, however, have such variations as pH, temperature, different types of water, etc. been taken into account. Enough has been done to show the importance of these factors. Powers (1917) showed that goldfish were killed in 14 hours by 1,282 ppm of sodium nitrate in distilled water, but 3,000 ppm did not injure them in in hard water. Downing (1954) reported on the influence of dissolved oxygen on the toxicity of KCN to rainbow trout. Doudoroff (1956) reported that fish could withstand more than 1000 times as much nickel cyanide at pH 8 as at pH 6.5. Henderson and Tarzwell (1957) emphasized the importance of these factors in investigating the toxicity of any given waste.

From these studies it becomes apparent that these physical variables influence the toxicity of many of the substances investigated. In some cases these effects may be traced to changes in the physiology of the fish used as test organisms, in others to differences in dissociation of the test material, and in still other cases to interaction of the toxicant with ions present in the water.

Recognizing the importance of these variables, this study was undertaken to determine whether some of these variables affect the toxicity of one poison. Sodium pentachlorophenate was chosen as the test poison for several reasons. It is an important industrial product, its basic effect on fish has already been investigated (Goodnight 1942), it is very soluble, and small differ-

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ences in concentration have marked effects on the relative toxicity.

METHODS

The fathead minnow (*Pimephales promelas*) was selected as the experimental animal. This species was chosen because it is readily available from nearby streams, is easily kept in the laboratory, and is of a convenient size. Once the minnows were brought into the laboratory they were held for several days in a tank provided with dechlorinated running water. During this period the fish were fed rolled oats, and any weakened or infected fish were removed. For 24 hours before being used as experimental fish no food was introduced. In this way only healthy vigorous unfed fish were used. The experimental fish were all of a similar size, averaging two inches in length.

To find the 24-hour TL_m (medium tolerance limit) various concentrations of sodium pentachlorophenate were used. In each test ten fish were placed in each concentration, and the number alive at the end of the 24-hour period was recorded. The ten fish were placed in three battery jars (three in two jars and four in one), each jar containing two liters of test solution. At no time during the tests was there evidence of discomfiture on the part of the fish due to crowding. Oxygen determinations were made throughout the time of the experiment to be certain that the supply was adequate. The tests were all run at a temperature of 15° C. This was the temperature the fish were previously acclimatized to in the laboratory. By using the same temperature for the tests, the shock of temperature change was avoided. The preliminary results were plotted on semilogarithmic paper in order to determine the appropriate concentration at which to run the subsequent tests. Once the range from total lethality to total survival was determined, five tests were run at each appropriate concentration.

It would have been preferable to run the tests for 48 hours, but the fouling of the water and pH changes that occurred after 24 hours made this undesirable. Furthermore these tests were made mainly to establish a base for later study of the effects of various factors on changing the toxicity of the sodium pentachlorophenate to the fish (Henderson and Tarzwell 1957).

The test solutions were made in the following manner. A 1% stock solution of sodium pentachlorophenate was made on a weight-per-volume basis (one gram of technical grade sodium pentachlorophenate dissolved in 100 milliliters of water). From this stock solution, a 0.1% solution was made, and an appropriate amount of this solution was pipetted into open-top battery jars. Water was then added to make the volume up to 2,000 cc. The water used in the test solutions was unchlorinated well water with a pH of 7.4–7.5. This well water had a total hardness of 400 ppm as $CaCO_3$ and a total alkalinity of 278 ppm as $CaCO_3$ as indicated by methyl orange.

In order to study the effect of various factors, one ppm of sodium pentachlorophenate was chosen as the test solution. This concentration was chosen because under most conditions it was lethal to fish in one-half to a few hours. This meant that the test could be finished before conditions had materially changed in the test solution. However, the test took long enough that changes in time due to the factor studied could be measured and compared.

In each test ten fish were used in three battery jars, each jar containing two liters of the one ppm test solution. The death of 50% of the fish was taken as the conclusion of the test in order better to standardize the results and to make statistical comparisons easier. Occasionally one or two fish would survive long after the majority of the experimental animals were dead. These unusually resistant fish were ruled out of this test by use of this 50% method. In most cases ten tests were made for each factor studied. Controls were run with all tests. These controls were treated in exactly the same way as the experimental animals except that the sodium pentachlorophenate was lacking in the solutions.

Tests for the effects of pH were conducted at 5.9–6.0, 7.5–7.6, and 8.9–9.0. The temperature selected for these tests was 18° C. In these tests the pH was checked by a battery-operated Beckman pH meter at the beginning and end of each experiment. The

pH was adjusted by the use of HCl or NaOH. In all these tests the oxygen concentration was checked by the Winkler method at the beginning and at the end. A concentration of three or more parts per million of oxygen is considered adequate for the fish (Henderson and Tarzwell 1957). At no time during the test did the oxygen concentration fall below this level.

The effect of temperature was determined by tests run at 10°, 18°, and 26° C. In these tests the pH was kept at 7.5–7.6 in all cases. In the experiments at the lower temperatures the pH had to be adjusted with HCl because of changes in the experimental solutions.

RESULTS

A series of carefully controlled tests was performed to determine the 24-hour TL_m of sodium pentachlorophenate for the fathead minnow (*Pimephales promelas*). These tests were conducted at 15° C in solutions of a pH of about 8. Preliminary runs indicated that all fish died at a concentration of about 0.4 ppm and that all lived at a concentration of about 0.2 ppm. Since there was such a narrow range between 0.2 and 0.4 ppm, it was difficult to obtain completely reproducible results. However, a number of tests indicated that the TL_m was between 0.32 and 0.35. Results of a series of such tests is given in Table 1.

TABLE 1. *Results of a series of tests to determine the 24-hour TL_m of the fathead minnow in various concentrations of sodium pentachlorophenate*

Concentration of ppm	Number of fish alive after 24 hours %
0.40	0
0.36	40
0.34	70
0.30	80
0.20	100

TABLE 2. *Survival time in minutes of 50% of fathead minnows at three different pH ranges in 1 ppm of sodium pentachlorophenate at a temperature of 18° C*

pH	5.9–6.0	7.5–7.6	8.9–9.0
Range of survival times	21–38	72–93	lived
Mean ± std. error	28.0 ± 1.7	80.7 ± 2.3	
Number of replications	10	10	5

TABLE 3. *Survival time in minutes of 50% of the fathead minnow at three different temperatures in one ppm of sodium pentachlorophenate, pH 7.5–7.6*

Temperature °C	10	18	26
Range of survival times	225–281	72–93	35–57
Mean ± std. error	260.4 ± 10.2	80.7 ± 2.3	46.0 ± 2.1
Number of replications	5	10	10

Tests for the effect of pH were conducted at three different ranges as indicated in the discussion of methods. The results of these tests are reported in Table 2.

Tests were conducted at three temperatures by the method discussed in the section on methods. These results are reported in Table 3.

DISCUSSION

The TL_m for the 24-hour period for sodium pentachlorophenate was determined by a series of tests to be somewhere between 0.32 and 0.35, although the extreme toxicity to fish made it very difficult to determine the exact TL_m. There is only a very narrow range between 0.2 where all the experimental fish lived and 0.4 where they all died. Because of this, very slight unavoidable differences in preparing the test solution and slight differences in the resistance of individual fish prevented the obtaining of completely consistent results. Differences that would be unnoticed with a less toxic material were greatly exaggerated in this narrow range.

The results obtained in the studies of the effect of pH on the toxicity of sodium pentachlorophenate were extremely interesting. The lower the pH, the more toxic the toxicant becomes to fish, as shown in Table 2.

Recently it has been found that the physiological effects of a given concentration of a phenol are correlated with its degree of dissociation (Blackman *et al.* 1955a and 1955b). In observing the activity of many substituted phenols on the mold *Trichoderma viride* and the green water

plant *Lemna minor*, Blackman *et al.* found that the physiological effect of a substituted phenol is greatest when the pH of the medium is closest to the pK value. They determined that the pK for pentachlorophenol is 4.8.

Investigations with fathead minnows indicate that as the pH approaches the pK value the toxicity of sodium pentachlorophenate increases. This finding has practical as well as theoretical importance. It shows that an alkaline river or stream could safely receive a higher concentration of sodium pentachlorophenate than a less alkaline one. The pH of a river or stream may show seasonal changes due to variations in rainfall or biological activity in the water. For these reasons the physiological activity of sodium pentachlorophenate may change from season to season in a body of water.

The results of the experiments on the effects of variable temperatures also demonstrated the importance of this factor in determining the toxicity of a given toxicant to fish. At a pH of 7.5–7.6 in a solution containing one ppm of sodium pentachlorophenate the mean survival time for 50% of the fish decreased as the temperature increased.

In the case of the temperature it can reasonably be assumed that the difference in survival time is due to the difference of the metabolic rate at the different temperatures. Since fish are poikilothermous animals, their rate of metabolism is directly dependent upon the temperature. At the greater metabolic rate at higher temperatures, the poisons would act more rapidly on the cells, and death would be sooner. This hypothesis is confirmed by the experimental results. These studies indicate that seasonal temperature changes are also an important factor in determining the amount of this material that may safely be released into streams.

These studies on the effect of pH and temperature demonstrate the importance of taking various factors into account in determining the toxicity of a given toxicant to fish. Frequently studies have been made on the toxicity of various industrial wastes to fish without investigating these and possibly other variables. As a result many published reports are not directly applicable to the conditions under which the toxicant may affect the fish.

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A Simple Counting Chamber for Nannoplankton[1]

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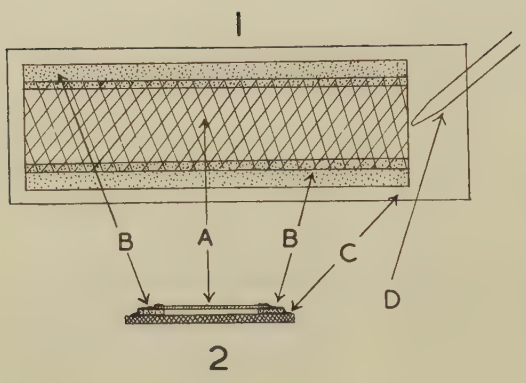
ABSTRACT

A simply made, cheap chamber for counting nannoplankton is described with detailed instructions for maintenance, use, and testing its accuracy. If certain precautions are taken the results of counts made therein are distributed according to the Poisson series. The chamber itself is simply a rectangular tube.

The inverted microscope technique developed by Utermöhl (1931a, 1931b, 1936; Lund, Kipling, and Le Cren 1958) is suitable for counting large and small algae, but if both are to be enumerated a very expensive microscope is necessary. In my view most of the counting chambers of the haematocytometer, Sedgwick-Rafter, or Kolkwitz type (for a review of methods of estimating algal numbers see Lund and Talling 1957), which can be used for nannoplankton on an ordinary microscope, are unsatisfactory, chiefly because the algae are not sedimented therein at random or because high-dry or immersion objectives cannot be used. In the case of nannoplankton the importance of random distribution is much greater than for larger algae, because if the distribution is otherwise, then the whole floor of the chamber has to be examined. This is not a serious matter when low powers of magnification are used to count relatively large objects, but when high ones are used for minute algae the time involved becomes large, because all these counting chambers are of considerable area. Then the disadvantage of estimating the size of populations by counting, which is so often cited, is indeed true. A further disadvantage of these chambers is that they must be machine-made with a high degree of precision; this is true also of the recently developed Palmer-Maloney (1954) slide.

[1] My grateful thanks are due to Miss C. Kipling for carrying out the statistical analysis, to Mr. H. C. Gilson who suggested using a dial gauge, and to Miss V. G. Collins and Mr. J. Doak who made the counts in the haematocytometer and on the inverted microscope in the test described on p. 63.

The present chamber, a rectangular tube, can be made with ease by anyone for the cost of a glass cutter, microscope slide, one or two long coverglasses, and a little cement. A dozen could easily be made in a day so that it does not matter if some have to be rejected or become broken. The exact depth to which it is to be made is not critical, though it is, of course, essential that any one chamber be of even depth throughout its working length. The algae within are distributed at random, and high-dry or immersion lenses magnifying forty to fifty times can be used. Much deeper chambers, suitable for examination under low-power lenses, can be made with equal ease, and one could probably be made for use with high-power immersion lenses, using a material thinner than coverglasses for the sides: such a chamber would probably be unsuitable for nannoplankton algae but might well be satisfactory for bacteria. If any form of inverted microscope is used there is obviously no difficulty in making bacterial counts, for the roofing coverglass now becomes the floor of the chamber. If the algae are killed in Lugol's solution, with or without the addition of acetic acid, the cells will soon come to rest on the bottom of the chamber and are not easily disturbed therefrom. Dr. J. McArthur has kindly tested the chamber and finds that it can be used on the revolutionary McArthur microscope (1934, 1947a, 1947b), and this means that it is possible to make counts anywhere in the world, on land, at sea, or in the air. This, of course, is not true of any preliminary concentration of the sample by sedimentation.



FIGS. 1 and 2.

FIG. 1. The chamber from above, and FIG. 2, in transverse section. *A* the roofing coverglass, *B* the supporting strips of coverglass, *C* the free margin of the microscope slide, and *D* the pipette in the correct position for filling the chamber. In Figure 2 the areas over which Araldite cement is smeared are shown solid, thicker black and, where it is on the outside, of uneven thickness. All details are in proper proportion except that in Figure 2 the thickness of *A* and *B*, and consequently of the chamber, is accentuated.

CONSTRUCTION OF THE CHAMBER

A microscope slide and long coverglasses, all scrupulously cleaned, are needed, the latter being shorter and narrower than the former; a length of about 6.5 cm and a breadth of 2–2.5 cm were used for the chambers I have made. The chamber is so made that the free area of the slide at one end is only 2 or 3 mm, while at the other end it is 5 mm or more (Fig. 1). The narrow free area is necessary to ensure that, when the chamber is full, the liquid will not make contact with the clips of a mechanical stage. The greater width of the free area at the other end of the slide permits the sample to be easily run in from a pipette. Two strips, about 5 mm wide, are cut from a coverglass. If each one is cut from an opposite side of a coverglass two straight edges, those of the coverglass itself, will be obtained and can be used to line the inner margins of the chamber. Such perfectly smooth margins are convenient rather than necessary. The rest of the coverglass, or another of different thickness, can be used to form the roof of the chamber. If a coverglass of the British type No. 1 is used for the margins the chamber will be about 150 μ deep, and if a No. 2 is used it will be about 200 μ deep. I use a No. 2 coverglass for the supporting margins and a No. 1 for the roof; then the chamber, from the top (upper side) of the roof to the floor is about 350 μ, so that there is an ample margin of safety with a lens of 450–600 μ working distance, such as the 3.75 mm $\times$ 50 water immersion of Cooke, Troughton and Simms Ltd., York, England, or the $\times$ 45 high dry of E. Leitz, Wetzler, Germany. An equivalent oil immersion lens is likely to have a shorter working distance so that even No. 0 grade coverglasses may be necessary. In my experience, however, a water immersion lens is quite as good as an oil immersion lens for this purpose.

The cement used is a liquid Araldite which can be obtained from Aero Research Ltd., Duxford, Cambs. (several other types are available). This consists of two solutions, Araldite 103 and Hardener 951, which are mixed together before use in the ratio of 10:1 by weight. The cement is not used until about thirty minutes after it has been thoroughly mixed but, as its setting time at laboratory temperatures is very long, there is no need to hurry; it is usually safe even after standing for three hours. The supporting strips are arranged as in Figure 1. There is no need for them to lie parallel to one another to make a usable slide, but it is a great advantage if the area of the chamber is to be measured in order to determine the depth of the chamber (p. 59). A little cement is smeared evenly along each long edge of the slide, and a coverglass strip slid on to and up and down each of them with the finger and thumb until all air bubbles have been expressed and the strips are separated from the slide by only the thinnest film of cement. Then the strips are arranged parallel to one another and about 5–10 mm apart (Fig. 1). Any excess cement lying between the strips and so on the floor of the chamber is wiped off, but any on the outside edge of the strip and along the margin of the slide is left, as this will help to make a secure union between slide, marginal strips, and roof of the chamber. The piece of coverglass which is to roof the chamber is now smeared similarly with cement to give a continuous film along its

outer long margins and carefully placed over the top of the also smeared marginal strips, so that very little or, preferably, none of the cement passes into the chamber. The upper surface of the roofing coverglass is smeared with more cement along the area overlying the sides of the chamber and further cement added if necessary to ensure that there is a continuous film from there over the free edge of the strip and onto the free edge of the slide (Fig. 2). A piece of thin paper is now put on top of the whole chamber, and the slide is placed in a press and left till the cement has hardened. There is no need for high pressure, 1–4 kg/cm^2 being ample. If the press is heated or kept in a hot place then the Araldite sets quicker, but the time recommended by the makers for such heating must not be exceeded. If the press is not heated, than it is advisable to heat the slide after it comes out of the press, as heated joints are stronger than unheated ones. After this curing, the slide is taken out of the press and placed in water until the paper cover is so soft that it can easily be removed. The parts of the paper along the outer edges of the chamber will have become impregnated with Araldite and so are not easily removed; indeed they are better left on as they strengthen and protect the chamber. If Araldite has passed into the central parts of the chamber it is best to discard the slide. If several chambers are made at once, as is most convenient, this does not matter. Should it be necessary to try to remove the Araldite, ordinary chromic-sulphuric acid cleaning mixture may be used, although this may dissolve the cement holding the chamber together. After the cleaning mixture has been in the chamber for some time, but before it is seen to be running under the edge, it is removed. A thin flat piece of metal (less than 200 μ thick!) is now carefully pushed into the chamber which has been filled with water in order to dislodge and remove the Araldite. If this cannot be done easily, cleaning mixture must be used again and the process repeated.

ALTERNATIVE MATERIALS AND METHODS

Smaller coverglass may be used, but the accuracy of counts made in such chambers is unknown as statistical tests have only been carried out on the type here described.

Any cement insoluble in the liquids used is suitable, but the only alternative I have used is polystyrene (see Lund 1951). The chamber is made in the usual manner, but the cement should not be hardened by heating above room temperature.

If a press is not available, a heavy, flat weight such as a block of metal is perfectly satisfactory.

DETERMINING THE DEPTH OF THE CHAMBER

1) Nearly all microscopes have a scale on the fine adjustment, and this provides the simplest method of determining the depth. However, in my experience, these scales, though allegedly correct to ± 1 or 2 μ, are commonly so incorrect, except possibly over some unknown or small portion of the total range, that they are useless. If this is found to be the case there are three simple methods by which the depth can be found.

2) If the chamber itself is free of cement, and its supporting strips completely cemented so that no water runs under the margins, its areas can be measured either by placing it over a piece of paper ruled in mm squares, or by placing some transparent material over it and cutting carefully and gently round the edges of the chamber with a sharp instrument such as a razor. Provided the material is of even quality, the weight of this piece can be compared with that of a known area of the material. This can be a very accurate method because of the delicacy of the balance and because a series of such areas can be cut out quickly enabling several weighings to be made. The long margins of the chamber will be easier to see if the Araldite is stained, as will be the case if the chamber is first left for some hours full of Lugol's solution. The volume of the chamber is determined by weighing the slide, first with the chamber empty and then filled with distilled water. For the first weighing the slide, if wet, should be dried by leaving it to stand in the laboratory. It will then be in equilibrium with the moisture in the atmosphere. For the second weighing any excess distilled water on the slide is removed with absorbent

paper. As water will be evaporating from the slide while weighing it, no very accurate determination is possible. However, the error involved is so small that it can be neglected. The weight of water in the chamber will be over 100 mg and the loss in weight should not exceed 100 μg, particularly with the modern balances which permit rapid weighing.

3) An engineer's dial gauge is fixed to one side of the microscope, in such a position that, when the objective is a little above the point at which the upper surface of the roof of the chamber comes into focus, a horizontal bar attached to the microscope behind the body tube makes contact with the plunger of the gauge. The reading on the gauge is taken when the underside of the roof of the chamber when filled is in focus and again when the floor is seen. A number of readings should be taken over the area of the chamber. The gauge should be accurate to ±2 μ.

If the chamber is clean it will be impossible to determine when the top and bottom are in focus. They can, however, be focussed as accurately as the microscope permits by the following procedure. The chamber is filled with a suspension of Indian ink (*e.g.*, 1–2%) in water and left to dry. Provided the suspension is not too thick there will be left a very thin film of minute particles on both surfaces. In order to be able to distinguish the floor from the roof of the chamber and so prevent breaking the slide when measuring the depth, the slide is filled with a thin suspension of familiar small particles, for example *Chlorella* cells stained in Lugol's solution. The errors of reading the dial gauge, of the gauge itself, and of focussing may be expected to be of the order of ±5 μ. There may also be small differences in the depth of the chamber from place to place either because it is not perfectly made, because the coverglasses used vary in thickness, or because the cement does. If several slides are made at once, as is easy to do, the best can be used. Even when I have found variations in depth by this method which seems to be beyond what might be expected, I have never been able to find any non-random distribution of particles in various parts of the chamber (concerning those areas adjacent to the open ends, see p. 63). In any case such differences will not lead to errors of any significance compared to those inherent in estimations of numbers per unit volume by counting. Equally, however, I reject any slide which is not found to be accurate by statistical tests which I apply if there is any doubt as to the perfection of the chamber. Variations in depth from unevenness in the thickness of the cement are unlikely because, if the procedure given here is followed, the layers are of insignificant thickness compared to the depth of the slide.

4) The chamber is filled with a suspension of easily recognisable small particles of known number per unit volume. Now, since the particles are distributed in the chamber in a random manner (p. 62) it is possible to compute their number per field, and so the volume of liquid in the area over which counts are to be made within a range which will be fixed by the number counted. *Lycopodium* spores are convenient since they are not too big (circa 25 μ diam.) and are exceptionally uniform, 1 mg containing about 94,000 spores (cf. Trease 1945, p. 753). *Chlorella* cells have also been used. In the case of *Lycopodium*, the number in the parent suspension can be determined relatively quickly by counting with an inverted microscope. It is necessary to add a little of a wetting agent if the spores are to be dispersed in water and some formalin to prevent fungal growths. Using low power lenses, more than one hundred spores can be counted per minute; and as the suspension can be kept forever, it is worthwhile counting a large number (*e.g.*, 10,000) to ensure a high degree of accuracy. *Chlorella* can be counted in a haemocytometer. It is best to do a few counts at a time, since if a large number are done in succession, the observer may become tired and so inaccurate. This is true of all counting (cf p. 62, and Dacie 1956, pp. 18–19).

This method is tedious if accuracy within small limits is required, but at the same time is one of extreme delicacy (cf. p. 65).

DELIMITATION OF THE AREA OVER WHICH COUNTS ARE TO BE MADE

The part of the field of view under the microscope over which counts are to be made is fixed by a square grid in the eyepiece. This is made very simply and its area must, of course, be known accurately in order to determine the volume of liquid in which counts have been made. In order to make counting quick, easy, and accurate, this area should be of such size that all of it can be seen at once without the eye having to move. If a 3.75 mm water immersion lens and a 15x eyepiece are used about 100 μ^2 is convenient. A ring of cardboard is cut out which fits onto the ledge (field stop) present within most eyepieces. It is coated with the Araldite or polystyrene cement, or any slow drying gum. A piece of soft glass rod is heated and pulled out so that a very fine rod results. Four pieces of this are broken off into suitable lengths and arranged on the disc within the eyepiece to form an approximate square. The scale on a micrometer slide is now focussed using the appropriate lenses and the grid tested for width and squareness. The final area is delimited by pushing the pieces of rod until a square of desired area is obtained. I find little difficulty in making one of exactly 100 μ^2, but so long as the grid is square the exact area is of little importance. The whole is now left to dry.

PROCEDURE FOR USING THE CHAMBER

The sample on which counts are to be made is treated with Lugol's solution and concentrated or diluted by a standard method (cf. Lund 1951; Lund, Kipling, and Le Cren 1958). Some of the liquid is then sucked into a pipette having a narrow end. This end is placed close to the open edge of the chamber which is farthest from the end of the slide (Fig. 1D) and allowed to flow out gently and continuously. It will run rapidly into the chamber until it overflows at the end where the pipette is. The chamber is placed on the microscope and left for some minutes (*e.g.* 5–10) to ensure that all the algae have sedimented. Then some distilled water is run onto the top of the slide and the algae brought into focus with the water immersion lens. Since the cells are distributed at random, the amount of time spent in counting depends on the accuracy desired. I generally examine 100–200 of these 100 μ^2 fields, though sometimes only 50–100 when there are many algae. For efficient, accurate, and quick counting the number of algae per field should neither be very large or small. For example, if only one species is under investigation, then an average of one to two individuals per field is sufficient for counting 100–200 algae, because, for these numbers, the expected variation is small enough to ensure that changes in the population equivalent to half a division of each cell (*i.e.*, $\pm 50\%$) can be determined (see also Lund, Kipling, and LeCren 1958). If counts of more than one species of alga are made, the total number of individuals counted will have to be increased more or less proportionately according to the degree of accuracy desired for each species. However, it is not advisable to have an average of more than five to ten cells per field because, with larger numbers, the time involved in recognizing and recording all the algae is usually greater than the results justify. If a range of volumes is taken for sedimentation from the sample collected, a suitable final concentration of algae is obtained and any preliminary test for this need only be cursory. No hard and fast rules can be laid down. It is a matter of commonsense, the golden rule being that counts should never be greater than are necessary to answer the question posed. It may seem that this is so elementary there is no need to say it, but I have all too often found workers devoting far more time to counting than is necessary.

CLEANING, REFILLING, AND MAINTENANCE OF THE CHAMBER

After a count has been made the chamber is cleaned as follows. Most of the liquid is removed by holding the slide in the hand and giving it a few sharp flicks. Then distilled water is run in under pressure by blowing from a bottle of distilled water or, better, by squirting water from a thin-

walled polythene bottle. Distilled water alone may not remove all the algae and other particles in the chamber, for once sedimented they are often difficult to move. Therefore the first wash with distilled water is followed by one with methanol from a similar polythene bottle, and finally the methanol is replaced by distilled water. Before the next sample is run into the chamber it is more or less emptied by flicking it by hand again. The chamber is next filled with some of the sample in the usual manner. Since this will be diluted slightly by the distilled water remaining in the chamber, it is discarded by flicking. The chamber is now ready for the second and final filling.

In time this washing procedure will not be sufficiently rigorous to clean the chamber thoroughly. It is then filled with a cleaning agent composed of 5 cc of hydrofluoric acid, 33 cc of nitric acid, 60 cc of water, and 2 cc of any detergent solution. This is a rapid and powerful cleaning agent which dissolves the surface of glassware. Hence it must be left in the chamber only long enough to ensure that no more than an extremely thin layer is removed, at the longest not more than 10–20 seconds. Therefore, it is almost immediately removed by flicking the slide as before, followed by half-a-dozen washes in distilled water. If it is left in too long or resorted to too frequently, the hydrofluoric acid will dissolve a thin layer of glass under the cement and finally loosen the joints of the chamber. All new slides are best washed with this mixture before their first use. Occasionally during the life of the chamber it should be filled with an aqueous solution of a dye to see if any runs under the margins. There is no harm in this provided the edges somewhere have a continuous, unaltered, layer of cement from one end to the other. If the chamber is cleaned in the recommended manner it should last for at least two years, even with frequent use.

STATISTICAL TESTS

The following are some of the tests that were carried out during the development of the chamber to ensure that accurate results could be obtained. Some of them are useful if for any reason there is doubt whether a chamber has been carefully constructed. In order to illustrate the variations in counts likely to be encountered, four chambers were made. The χ^2 test for randomness was used.

1) Counts were made of two lots of *Lycopodium*, each comprising 1000 spores, from a standard suspension by the methods described earlier. Counts were made over 50 to 200 fields for each filling of the chamber, and the fields themselves were distributed over the chamber in a more or less random manner, the areas adjacent to the openings being avoided (see below). The counts considered singly or in groups of ten were found to be distributed at random. The differences in depths at different points in the chamber observed when using a dial gauge (p. 60) were therefore either not real, that is there were errors of the instrument and the manipulation of it and the microscope, or, if they were in part real, they were so small that their effects on the distribution of the spores were insignificant. In the course of this test it was found that if the chamber was not filled by one release of water from the pipette, that is by continuous flow, small but significant errors could result. However, unless a pipette of very fine bore, such as a capillary one is used, it is difficult not to fill the chamber with one release of water. I also found that if I did a large number of counts one after the other my accuracy decreased (cf. Dacie 1956, who also discusses other "human" errors which may arise in counting).

2) A series of counts was made on successive sub-samples from a parent suspension. Each time, after a count had been made, the slide was emptied, washed, and refilled by the procedure here described. *Lycopodium* spores, *Chlorella* sp., and *Ankistrodesmus falcatus* (Corda) Ralfs var. *spirilliformis* G. S. West were the test objects. In all three cases the counts were distributed in a random manner. This result confirms the previous one and shows that objects of varied size and shape covering most of the range of nannoplankton can be estimated with this chamber.

3) Counts of *Ankistrodesmus falcatus* var.

TABLE 1. *Counts of* Chlorella *cells analyzed in sets of ten consecutive fields and in individual fields* The distributions in the two slides are *not significantly* different from random, nor were they different from those in the central areas of the chambers. Fields 1–30 along one side and 31–60 along the other.

Slide D							Slide B						
Fields							Fields						
1–10	11–20	21–30	31–40	41–50	51–60	Mean	1–10	11–20	21–30	31–40	41–50	51–60	Mean
6	5	3	4	2	4		2	3	3	7	4	5	
1	1	8	1	0	3		1	4	1	4	0	0	
3	7	2	4	2	4		3	2	1	2	3	5	
5	3	3	2	5	1		5	5	7	1	1	7	
1	5	2	0	3	2		4	3	0	3	6	5	
4	1	2	4	2	6		1	3	3	3	4	3	
1	1	4	2	2	1		2	3	1	3	3	3	
0	1	1	0	1	2		3	1	3	2	2	1	
6	2	5	2	2	4		1	2	2	3	1	1	
0	2	3	3	2	4		4	1	0	5	4	5	
Total 27	28	33	22	21	31	27.0	Total 26	27	21	33	28	35	28.3

spirilliformis were made in a haematocytometer by the method described in Lund (1951; see also Lund, Kipling, and Le Cren 1958), by the normal inverted microscope technique, and by the present method. There was no significant difference between the results obtained. There is, therefore, no systematic error in the present method, such as, for example, the loss of a percentage of the cells outside the chamber when filling it.

4) Counts were made, first with *Lycopodium* and later with *Chlorella*, close to and parallel with one margin of the chamber (Table 1). Then additional such counts were made at intervals across the slide, the last being close to and parallel with the opposite margin of the chamber. Alternatively counts were made along each margin of the chamber and compared with those in the center as in the examples here quoted. The distribution of the counts was at random. Cells do not, therefore, tend to be more or less aggregated near the edges. Nevertheless, I think it is possible that the distribution could be non-random close to the edge if this were rougher than in the chamber I used. Roughness may arise if the outer straight edges of a coverglass are not used for the margins of the chamber, that is if the inner margin is one which has been cut in making the strip (see p. 58). It may also arise if the cement protrudes too much and too irregularly into the chamber. Therefore, as a general safety precaution counting is best done in fields not immediately adjacent to the margin.

5) Counts were made with *Lycopodium* spores and *Chlorella* cells along the whole length of the chamber and grouped into tens to see if there were any significant differences in the distribution of the means. The examples quoted here are typical of the results obtained (Table 2).

If the ends were avoided, the distributions in all were not significantly different from random. In the four examples given here, if the counts close to the ends were included, some distributions were obtained which were significantly different from random (slides Ca, D). This was not always the case (*e.g.*, B, Cb and A).

Ca and Cb are counts made with the same chamber in two separate fillings. A t test shows no significant difference between the means. The same stock suspension of *Chlorella* was used in each case. Since one gave a distribution significantly different from random and the other did not, it would seem that non-randomness is a function of the overall technique, and not of imperfections in the method of making the slides. In some cases (*e.g.*, slides B and A), though the distributions were not significantly different from random, there seemed

TABLE 2. *Counts of* Chlorella *cells and* Lycopodium *spores (Slide A) from one end of a chamber to the other, analysed in sets of ten consecutive fields and in individual fields*

Slide Ca

Fields											
1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	100–110	Mean
1	3	2	0	1	6	0	2	2	2	1	
3	0	3	8	3	3	4	8	2	6	4	
0	1	1	4	2	4	6	4	2	7	3	
2	2	6	5	5	3	2	0	4	1	4	
3	0	2	2	4	4	2	4	4	3	3	
1	3	6	1	3	5	1	4	0	9	4	
2	1	2	3	7	0	1	3	8	0	2	
5	3	2	3	5	1	2	5	3	3	2	
1	4	1	3	3	6	2	4	2	5	4	
4	3	3	2	3	1	3	2	4	3	6	
Total 22	20	28	31	36	33	23	36	31	39	33	30.2

Slide Cb

Fields								
1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	Mean
3	2	4	6	3	5	1	8	
3	3	3	2	5	3	0	4	
1	1	3	3	5	2	2	2	
2	0	4	4	3	1	4	1	
3	3	3	2	4	4	4	2	
5	1	6	0	3	3	3	3	
1	4	4	2	3	6	4	1	
2	3	4	4	1	1	2	3	
5	2	5	3	2	2	1	4	
0	2	2	4	3	1	4	4	
Total 25	21	38	30	32	28	25	32	28.9

Slide B

Fields											
1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	100–110	Mean
2	1	2	1	1	3	1	4	6	3	3	
0	2	0	5	7	1	2	5	0	3	4	
0	3	4	1	4	8	4	3	1	5	2	
7	5	3	2	5	4	1	2	4	2	7	
4	2	5	3	1	4	1	3	3	8	3	
2	2	2	2	2	0	5	2	1	3	2	
2	2	2	3	1	3	4	2	3	2	5	
1	2	5	5	0	2	1	1	3	2	4	
6	4	2	2	1	3	2	3	2	2	4	
1	5	2	4	3	2	5	0	4	2	8	
Total 25	28	27	28	25	30	26	25	27	32	42	28.6

Slide D

Fields								
1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	Mean
1	1	3	7	5	5	2	6	
3	1	4	4	3	0	7	2	
1	3	1	3	6	4	2	2	
2	0	1	3	3	4	3	2	
5	2	7	5	1	1	2	8	
1	1	3	2	2	3	3	2	
1	4	4	2	0	1	3	7	
1	1	1	0	5	4	3	0	
4	0	2	2	1	1	0	5	
3	1	1	3	8	2	2	5	
Total 22	14	27	31	34	25	27	39	27.4

Slide A

Fields					
1–10	11–20	21–30	31–40	41–50	Mean
6	9	16	7	11	
11	9	7	5	8	
12	9	3	11	2	
15	5	7	13	6	
15	9	7	4	10	
7	6	7	12	4	
9	12	10	13	5	
10	12	8	4	6	
8	9	7	6	12	
9	4	14	14	10	
Total 102	84	86	89	74	87.0

to be a tendency for higher or lower counts in the fields near the ends of the chamber. Therefore counts should not be made over a distance of one centimetre from each end of a chamber 6.5 cm long. If a preliminary statistical check is made it may well be found that counts can be made even nearer the ends, but the chambers are so large that I have never needed to count near an end.

6) Counts were made with a *Lycopodium* suspension on a chamber cemented with polystyrene which had been much used. Filling with methylene blue solution showed that some of the cement lying between the roof and supporting strip on one side of the chamber had gone. A count of 1000 spores was compared with another made when the chamber was new. There was a significant difference between the two counts. The means, however, only differed by 3%. This provides a good example of the great sensitivity of counting for testing such a chamber.

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The Origin and Distribution of Phosphorus in Western Lake Erie

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ABSTRACT

The phosphate phosphorus distribution in western Lake Erie in May 1951 and the average concentration throughout 1950–1951 are shown to be a result of the drift current pattern and the discharge of the Maumee and Detroit Rivers. The bed rock in the lake appears to provide negligible quantities. The Detroit River supplies 405 metric tons per year at an average concentration of 2.6 μg PO_4-P/L, and the Maumee River supplies 125 tons at an average concentration of 43 μg PO_4-P/L. The remaining streams supply 39 tons at a concentration of 16 μg PO_4-P/L. There is a loss of soluble phosphorus, possibly as precipitating ferric phosphate and by adsorption onto ferric hydroxide. The bottom sediments are considerably enriched in phosphorus.

Phosphate phosphorus and turbidity in the lake are positively correlated ($r = +0.65$), and evidence from turbidity data indicates that the lake is enriched by a thin-layered tongue of water from the south shore streams which flow over or under the clearer, nutrient poor water, and then mixes vertically with it.

Removal of fish by man accounts for an annual loss of 29 metric tons, or six per cent of the average annual input of phosphorus. Approximately 94 metric tons, 20 per cent of the average annual input, may be held temporarily as phytoplankton.

Although phosphorus is probably never limiting in the southern waters of western Lake Erie, the accompanying turbidity sometimes prevents any significant phytoplankton growth.

INTRODUCTION

Phosphorus is a relatively scarce element in the earth's crust, averaging less than 0.05 per cent by weight. There have been many studies on the occurrence of phosphorus in natural waters (Juday *et al.* 1928, Juday and Birge 1931, Wiebe 1931, Cooper 1938, Armstrong and Harvey 1950, Odum 1953). In Lake Erie, Chandler and Weeks (1945) investigated the occurrence of phosphorus in the western basin in relation to phytoplankton production. Because of its physiological importance, such relationships have been investigated repeatedly in many parts of the world.

Although phosphorus is an important microelement in the nutrition of aquatic plants it is frequently present in fresh water in such quantity as to become a relatively conservative element, despite variations in concentration due to biological activity. Depending upon the nature of the sources, the morphology of the basin, and the climatic conditions, the concentration and distribution of phosphorus may undergo seasonal cyclic changes.

It is the purpose of these remarks to describe the nature and magnitude of these changes in western Lake Erie.

I am grateful to Dr. Jacob Verduin for valuable criticism and Dr. Thomas H. Langlois who placed the facilities of the F. T. Stone Institute of Hydrobiology, Put-in-Bay, Ohio, at my disposal. The work was conducted under a fellowship furnished by the Ohio State Conservation Department.

METHODS

Thirty-two one-day sampling cruises were made in 1950–1951 in western Lake Erie. The cruises averaged 80 to 112 kilometers in length and followed several different routes (Fig. 1). Samples were taken at eight-kilometer intervals with a bucket from near the stern of the moving boat where turbulence insured mixing to at least half a meter. Sub-samples were stored in the dark in acid-washed glass bottles. Ashore, samples were stored at 7° C until analyzed, which was customarily within twelve hours. Samples kept under these conditions showed an

[1] The present address of the author is: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.

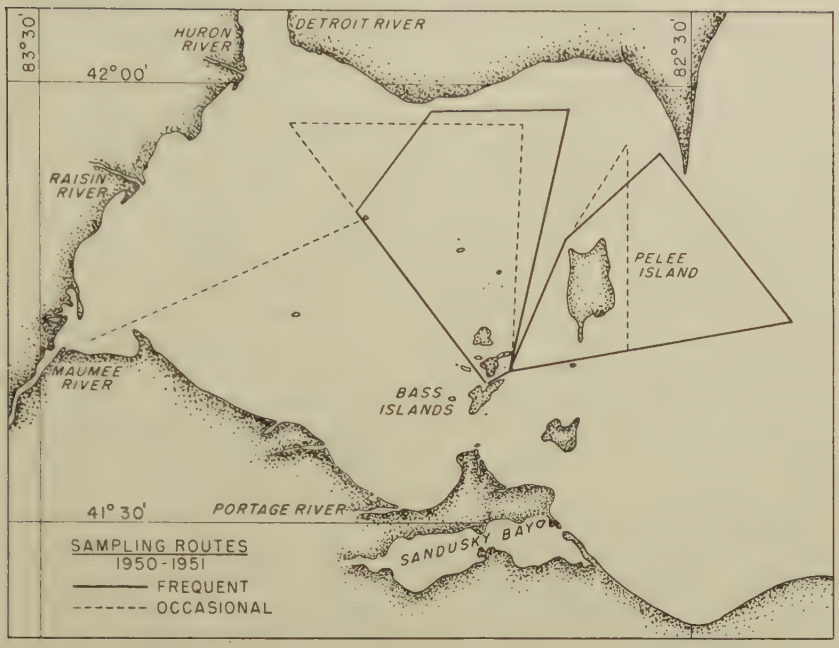

FIG. 1. Sampling routes followed in western Lake Erie from July 1950 to June 1951.

apparent decrease of phosphate phosphorus not exceeding 1.2 μg/L in twenty-four hours.

The technique of mobile sampling was adopted as a result of Verduin's (1951a) studies. In order to cover as large an area as possible in the time available only surface samples were taken. This decision was based in part on Chandler's (1940) finding that the western basin of the lake is ordinarily unstratified.

Denige's method as modified by Atkins (1923) was used for phosphate phosphorus. Just before analysis the sample was filtered through *Reeve Angel* 202 filter paper. The method of Robinson (1941) involving the use of perchloric acid was used for the analysis of total phosphorus.

Samples of very turbid Lake Erie water were permitted to settle completely. After pouring off the supernatant liquid the residue was dried, weighed, and resuspended to form turbidometric standards. Determinations were made in a spectrophotometer at wavelength of 600 mμ. Turbidity reported as parts per million (ppm) refers to the actual weight of suspended matter.

OBSERVATIONS

The sources of phosphorus

The river systems drain two main regions. The Detroit River drains Lake Huron via Lake St. Clair. The remaining rivers drain the western and southern watersheds of Lake Erie. These rivers are the Maumee, Sandusky, Portage, Raisin, and Huron. Hydrologic data for each river are summarized in Table 1.

The Detroit River provides 96 per cent of the total discharge into Lake Erie. The average concentration of phosphorus in this river is quite low, however. Samples taken at the mouth of the Detroit showed a range of 0.0 to 4.6 μg PO_4-P/L and a mean of 2.6 μg PO_4-P/L.

The southwestern drainage area is dominated by the Maumee River, which provides slightly less than 3 per cent of the total discharge into the lake. All the other rivers combined contribute 1.5 per cent of the total discharge. Analyses for phosphate phosphorus are available for all these rivers. The Maumee River contributed an average of 43 μg PO_4-P/L in 1945, including

TABLE 1. *Analyses of water from tributaries to western Lake Erie during high and low river stages*

River	River stage			
	Low 15 Aug. 1950		High 13 March 1951	
	μg PO_4-P/L	ppm silt	μg PO_4-P/L	ppm silt
Huron	7.0	25.0	15.0	15
Maumee	—	—	94.5	111
Portage	—	—	62.3	36
Sandusky	10.0	9.5	20.0	40
Average	8.5	17.2	47.9	50
Average, excluding Maumee R.			32.4	30

Grand average south shore streams, exclusive of Maumee: 22.8 μg PO_4-P/L; 25.1 ppm silt.

TABLE 2. *Discharge data and phosphate phosphorus input of tributaries to western Lake Erie*

River	Drainage area km^2	Average discharge m^3/sec	Yield m^3/sec/ha	% of total discharge	Average[1] phos. conc. μg PO_4-P/L	Total yearly input metric tons	% of yearly total
Detroit	—	4,900.0	—	95.8	2.6	405.0	71.5
Huron	2,305	16.0	0.694	0.3	11.0	5.6	1.0
Raisin	2,640	18.8	0.712	0.4	15.0	9.0	1.6
Maumee	17,070	132.7	0.777	2.7	43.0	125.0	22.0
Portage	1,520	11.0	0.724	0.2	22.8	8.0	1.4
Sandusky	3,680	29.8	0.809	0.6	15.0	14.2	2.5
Totals	27,215	5,108.3		100.0		566.8	100.0
Average					18.2		

[1] Estimated in part from Table 1.

the contribution from the City of Toledo (Curl 1957). The data for the remaining rivers are less extensive (Table 1). If they can be assumed to be representative, the average contribution of the southwestern rivers, exclusive of the Maumee, is 22.8 μg PO_4-P/L or approximately half that of the Maumee. On the basis of these figures, total discharge of phosphate phosphorus into western Lake Erie may be computed (Table 2). The total yearly discharge is 567 metric tons, 71.5 per cent of which is supplied by the Detroit River. The Maumee River, however, which supplies 22.0 per cent of the total phosphorus, is the source with the greatest concentration.

TABLE 3. *Analyses of bottom sediments for total phosphorus and apparent concentration factors for sediments*

Location	mg P/g mud	20 ppm turbidity suspension[1] mg P/L	Conc. factor[2] of soluble P	Conc. factor[3] of total P
Maumee	76.7	1.5	58	16
Maumee	52.5	1.0	39	11
S. Bass Is.	53.7	1.0	39	11
S. Bass Is.	45.0	0.9	35	10
Average	56.9	1.1	43	12

[1] If sufficient mud were resuspended to make 20 ppm turbidity, total phosphorus content would be figures in column.

[2] Using average figure from Table 4 for soluble phosphate when turbidity was 20 ppm.

[3] Using average figure from Table 4 for total phosphorus when turbidity was 20 ppm.

TABLE 4. *Soluble and total phosphorus content of water samples containing approximately 20 ppm turbidity*

Date	Turbidity ppm silt	PO_4-P μg/L	Total P μg/L
3/7/51	16	38.0	80
4/6/51	26	25.3	112
4/6/51	18	24.5	93
4/6/51	19	15.8	89
Average	19.7	25.8	93.0

The rock basin of the lake (overlayered in some places with up to one hundred feet of sediment) contains an insignificant amount of phosphorus. This rock, consisting of limestones and dolomites, crops out in the center of the basin to form a series of islands. Analyses of the dolomite forming South Bass Island showed an average of 0.035 per cent P. To produce a solution containing 10 μg P/L (the average soluble P in the lake), approximately 0.028 g of rock/L would have to be dissolved. If the assumption is made that all of the calcium carbonate hardness of the lake (averaging 90 ppm) is due to solution of bed rock, 32 μg P, or three times the average concentration, could be accounted for. However, all the south shore streams themselves have hardness well over 100 ppm, and it seems unlikely that much phosphorus is derived from bed rock solution.

To evaluate the role of bottom sediments in controlling phosphorus distribution, several sediment samples were taken from the

Maumee River estuary and in the Bass Island region. These samples were analyzed for their total phosphorus content. Each sample consisted of a core about 30 cm in length which was thoroughly mixed and subdivided. Analyses (Table 3) show an average of 56.9 mg P/g of dried mud. If sufficient mud from each location was resuspended so that a turbidity of 20 ppm resulted, an average of 1.1 mg P/L would be dissolved and in suspension. This is twelve times the amount of total phosphorus normally associated with 20 ppm turbidity and forty-three times the soluble phosphorus found under the same conditions (Table 4). Since the phosphorus content of the sediments is larger in amount than that normally associated with the same weight of particles when in suspension, there must be enrichment from the soluble fraction in the overlying water column even when little inorganic suspended matter is present.

The distribution of phosphorus

The horizontal distribution of phosphorus is depicted in Figures 2a, b, and c. Sampling was curtailed by winter ice cover or bad weather. Therefore the data are selective in that the only cruises yielding contourable results occurred in early summer of 1951; other cruises did not cover a sufficiently large enough area or in fine enough detail to permit contouring.

On April 27, 1951, a tongue of water with less than 1.0 μg PO_4-P extended southward along the west coast of Pelee Island. A tongue of phosphate enriched water extended into the island region from the southwest and up along the east side of Pelee Island. The maximum value of 10.8 μg PO_4-P was found in the Bass Islands region. The 15 ppm isopleth of turbidity followed the 5 μg phosphate isopleth rather closely.

On May 31, 1951, a tongue of water with no detectable phosphorus extended from the mouth of the Detroit River to an area between Pelee Island and the Bass Islands. The water to the northeast of the tongue had very little phosphorus (1.2 μg PO_4-P/L). The water to the southwest intrudes into the tongue as a series of fingers. The maximum value found was opposite the mouth of the Maumee River (10 μg PO_4-P/L). Tur-

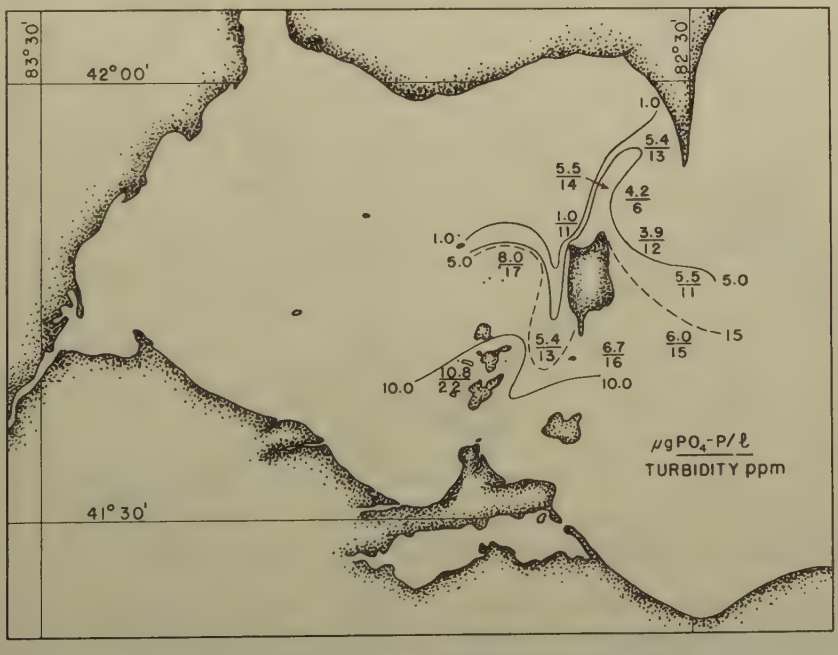

FIG. 2a. Horizontal distribution of PO_4-P and turbidity in the Bass Islands region of western Lake Erie on 27 April 1951. Dashed line indicates turbidity distribution, full lines indicate phosphorus distribution.

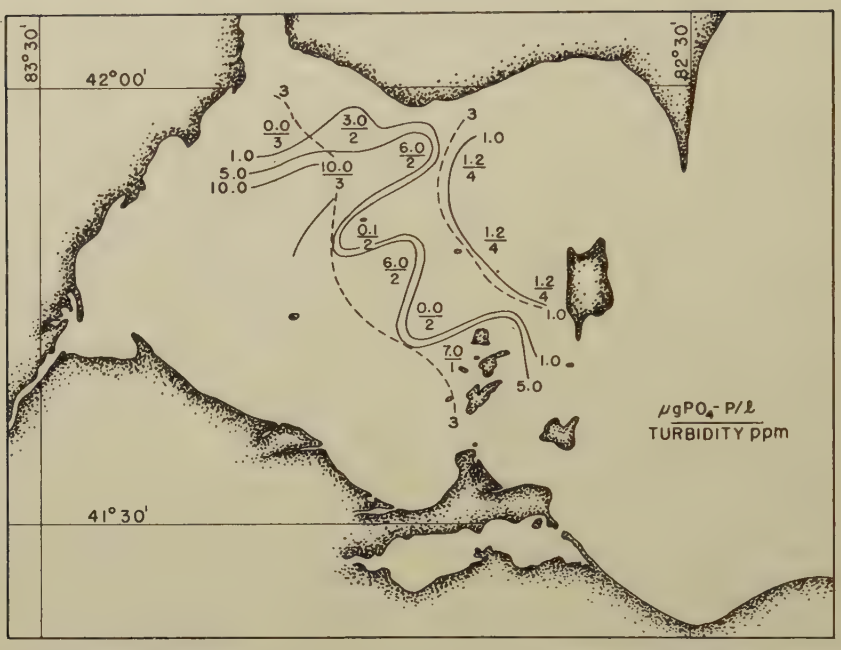

FIG. 2b. Horizontal distribution of PO_4-P and turbidity in western Lake Erie on 31 May 1951. Dashed lines indicate turbidity distribution, full lines indicate phosphorus distribution.

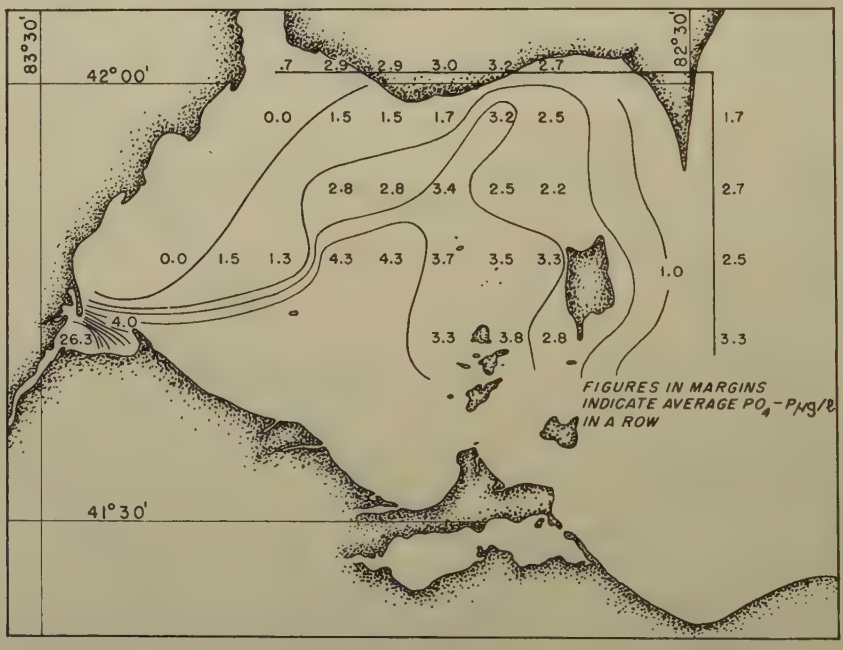

FIG. 2c. Horizontal distribution of averaged PO_4-P in μg/L in western Lake Erie in May 1951.

bidity values ranged from 1 to 4 ppm over the area sampled, with no significant differences between areas of high and low phosphorus concentration.

The averaged distribution of phosphorus in May 1951 (Fig. 2c) showed the greatest concentration in the southern and central waters of the basin. Averages of horizontal

TABLE 5. *Comparison of phosphate phosphorus and turbidity at various depths on November 14, 1950, in vicinity of Bass Islands*

Depth m	PO_4-P µg/L	Turbidity ppm
Surface	15.0	36.4
2.2	14.8	36.0
7.0	19.5	42.0
9.0 (bottom)	28.5	68.0

and vertical columns are given at the top and to the right of the figure to show this more clearly. The greatest phosphorus concentration (26.3 µg PO_4-P/L) occurred at the mouth of the Maumee River. There was no detectable phosphorus in a band eight miles wide, extending from just north of the Maumee River estuary northeast to Point Pelee. A tongue of phosphorus-enriched water extended in a northeasterly direction across the center of the basin.

Soluble phosphorus and turbidity were often higher near the bottom, as on January 25, 1951. Ice cover was present but water movement could have been caused by density currents or seiche action. In 10 meters of water a sharp transition was found at 5 meters depth. Above 5 meters the phosphorus concentration was 8.3 µg PO_4-/P/L, and the turbidity was 13 ppm. Below 5 meters the phosphorus concentration was 15.0 µg PO_4-P/L, and the turbidity was 40 ppm. On November 14, 1950, turbidity and phosphorus were stratified without benefit of ice cover (Table 5).

Since turbidity values and soluble phosphorus concentrations seemed to show some correspondence, all the available data for the simultaneous sampling of these two variables in western Lake Erie have been plotted in Figure 3. A significant (at the 5% level by *t*-test) correlation coefficient of $r = +0.65$ indicates a low positive correlation. A least-squares regression line fitted to these data has the formula: Phosphorus = 0.56 turbidity +0.51. However, the standard error of estimate of $S_x = 3.78$ for this expression indicates that it would be useless to attempt prediction of soluble phosphorus values from turbidity measurements.

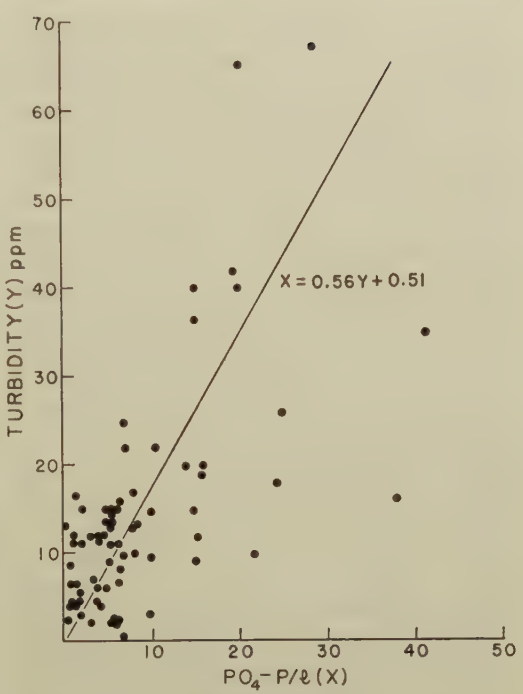

FIG. 3. Regression plot of turbidity and PO_4-P in western Lake Erie.

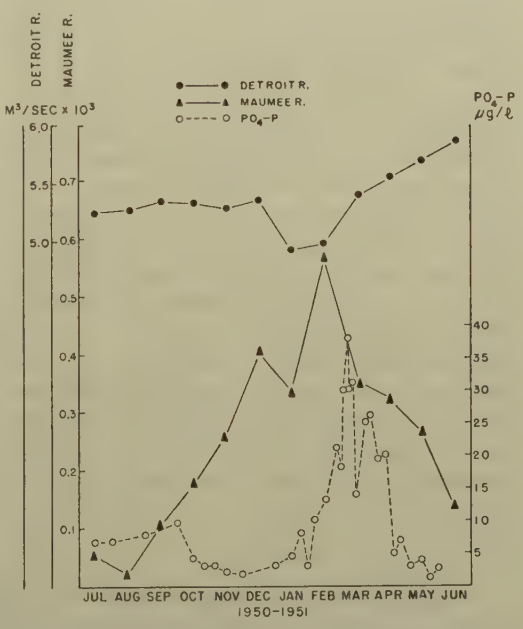

FIG. 4. Monthly average discharge of the Detroit and Maumee Rivers in cubic meters per second and average PO_4-P in µg/L in western Lake Erie from July 1950 to June 1951.

The soluble phosphorus data for all the trips in each month have been averaged and are presented in Figure 4, together with monthly average discharge data from the Maumee and Detroit Rivers for the same period. There is a general correspondence between the Maumee discharge and phosphate values except during the period October 1950 to February 1951. The phosphate curve shows a decided deflection at a time when Maumee River discharge is increasing. Since phosphate phosphorus concentrations normally rise with increasing stream flow (Slack 1955, Curl 1957) this must be considered an anomalous result. Furthermore, there was an increase in the Detroit River discharge from 5.24×10^3 m^3/sec to 5.35×10^3 m^3/sec during the period from July to December 1950, whereas the Maumee River discharge increased from $.057 \times 10^3$ m^3/sec to $.400 \times 10^3$ m^3/sec in the same period. If conditions obtaining in July can be assumed to be in a steady state, then the net change in the ensuing five months is relatively greater flow by the Maumee River and supposedly higher phosphate levels in the lake. Since this is not the case, and since most of the basin was sampled within a month's time (the average flushing time is two months), then it appears likely that the phosphate rich Maumee River water is going under the poorer Detroit River water. A relatively higher load of suspended matter and relatively colder temperatures of the Maumee River would bring about such a condition. The Maumee River does have a higher sediment load than the lake water into which it flows (Lamar 1953).

Since the sampling of surface water only was predicated on a previously demonstrated homogeneity of the water column, the occasionally anomalous correlation of Maumee River discharge and lake phosphate is not surprising.

DISCUSSION

Almost all the phosphorus in the western basin of Lake Erie probably has had an allochthonous origin. Loss from the drainage areas occurs by solution, sediment inwash, and domestic pollution. Temperature, precipitation, and farming methods will determine the time and amount of phosphorus lost to the lake.

The largest total amount of phosphate phorphorus is brought in by the Detroit River but in very dilute solution. The Maumee River is the largest source of concentrated phosphate phosphorus.

Some phosphorus may at times be dissolved from either suspended or bottom sediments. Naturally, such a process can best take place when the particles are in suspension. The largest sized particles, while perhaps containing the most phosphorus per particle, settle out rapidly and tend to stay in place. Some of these sediments may be moved into the lake by saltation during periods of increased discharge and turbulence. Regeneration of phosphorus from such sediments would be more likely to take place in Maumee Bay than in the lake. In the bay, anaerobic conditions occasionally occur at the surface (Lamar 1953) and most certainly prevail at the bottom (Brown 1953). Such conditions would permit release of phosphate phosphorus (Einsele 1936). In the lake proper, oxygen levels are high from surface to bottom except under very unusual circumstances. This would tend to favor retention of phosphorus in the sediments as well as precipitation of phosphorus combined with ferric iron. Maumee River water averaged 50 μg Fe^{+++}/L in 1950–1951, which could be present as hydroxide or as ferric phosphate. In the latter state 50 μg of iron would be combined stoichiometrically with 27 μg of phosphorus. In an excess of ferrous ion, ferric hydroxide would also be formed and phosphate ions could be adsorbed onto the colloid, and the complex would then precipitate. A mechanism such as this would account for the high phosphorus values of the lake sediments. If 27 μg of the average of 43 μg PO_4-P/L in Maumee River water were to be combined as ferric phosphate and lost by precipitation to the river and estuary bed, 16 μg would remain. In the spring of 1950 there was virtually no biological activity to remove phosphate, since a phytoplankton bloom did not develop. There was an average of 11.9 μg PO_4-P/L in the surface waters of western Lake Erie in 1950–1951. The average difference of 4

μg/L could have been contributed to the sediments in the western basin. On the basis of the Maumee River flow alone this amounts to 8.8 metric tons per year. Ferric iron in the other south shore streams was comparable to that in the Maumee River, and, using the same treatment as above, their total contribution is about 2.6 metric tons per year, or a grand total of 11.4 metric tons. Clarke (1916) gives the iron content of the Detroit River water as 45 μg/L. The figure is probably somewhat higher today. This amount of ferric iron could combine with 25 μg PO_4-P. Since the Detroit River water averages only 2.6 μg PO_4-P/L both in the river and in the lake, it must be concluded that most of the iron is present as the hydroxide. If any of this phosphate is lost to the sediments, it must be by adsorption onto the colloidal hydroxide. The amount thus lost is probably trivial. If these figures are correct, then of the some 567 metric tons of soluble phosphorus coming into the lake yearly from tributaries, approximately 62.7 per cent of the southshore contribution or 102 tons could be precipitated out as ferric phosphate fairly close to shore and another 11.4 tons could be adsorbed onto ferric hydroxide and precipitated out in the center of the basin. While these losses would decrease the total addition of phosphate phosphorus to the lake from 567 tons to 454 tons per year, they concern only the southern tributaries, whose contribution would be decreased from 163 tons to 50 tons, a loss of 69.3 per cent. None of these figures concerns the addition and loss of insoluble forms of phosphorus. Even with the problematical losses indicated above, there still remains sufficient phosphorus in solution to support large phytoplankton blooms.

Although the data on horizontal distribution are limited, the patterns shown in Figure 2 are consistent with what is known of the sources of phosphorus. However, the patterns must be influenced by drift currents as well as the placement of sources. Unfortunately, the drift currents of the western basin are poorly known. Harrington (1895) used drift bottles, and Olson (1950) and Verber (1953) used drift cards (Olson 1951) to measure the surface currents. Verber (1953) established that the card studies indicated wind driven surface currents which averaged 6.5 miles per day. Both Harrington's (1895) and Olson's (1950) results are very similar and may be taken

FIG. 5. Current chart of western Lake Erie. Taken from Harrington (1895) and Olson (1950).

as a picture of the mean surface drift in the western basin. A generalized current chart (Fig. 5) postulates that part of the Detroit River water, passes down the west shore and part flows eastward through the northern passage, where a portion describes a gyre around Pelee Island. Maumee River water, in its eastward flow, is incorporated into the gyre and also passes out through the southern passage. There is reason to believe that the flow pulsates in response to seiche action (Verber 1953), with a resulting net outflow through the northern passage. The averaged chart of phosphorus distribution for May 1951 (Fig. 2c) is a reflection of this current pattern. The proposed gyre around Pelee Island is not evident in this chart.

Although phosphorus and turbidity are positively correlated, their biological effects are opposed. Thus, the paradoxical situation occasionally exists in the western basin in which the decrease in light penetration caused by high turbidity completely offsets the potential benefit of high phosphate concentration. This happened in the springs of 1950 (Verduin 1951b) and 1951 (Curl 1951).

Recourse has been made above to water temperature and sediment load as factors explaining the low phosphorus values experienced in the October to February period. Some circumstantial evidence exists for this interpretation. Verduin (1953) indicates that the turibidity injected into the lake by Ohio tributaries influences a much greater area than would be indicated by the volume of discharge. He postulates that the silt laden river water might flow in a thin layer over or under the clear lake water and then mix vertically, muddying a large area.[2] Because the data were not available at the time of writing, Verduin was unable to verify his hypothesis. It is now possible to make the calculations. Verduin estimated a sediment load of 32×10^4 metric tons in an area of turbid water encompassing 2,940 square kilometers and containing 29 cubic kilometers. This estimate was based on an average turbidity of 11 mg/L in the turbid region found in sampling trips taken during April 27 and May 2, 1951.

In March and April the Maumee, Portage, and Sandusky Rivers had a total discharge of 2.2 cubic kilometers and a total sediment load of 364,000 metric tons (Lamar 1953). This is equivalent to 165 mg/L turbidity. If this volume is diluted (some thirteen fold) to 29 cubic kilometers then the average turbidity would be 12.6 mg/L, a figure close to the observed 11 mg/L. The difference may be attributed to loss of some sediment at river mouths and to the general nature of the computation. Since high concentrations of phosphate phosphorus and suspended sediment have common origins, it may be concluded that western Lake Erie is fertilized by rapid horizontal flow of a thin layer of water followed by vertical mixing. This phenomenon would also account for anomalies of river flow and phosphorus concentration.

In addition to phosphorus loss by precipitation of ferric phosphate a portion is removed semi-permanently by biological activity. The rest of the phosphorus is carried into the central basin of Lake Erie. An estimate may be made of the amount removed by man. From 1935 to 1945 the average yearly commercial catch of fish in western Lake Erie was 13,430 metric tons. Atwater (1885) gives the ash content of five species of fish, which make up the bulk of the Lake Erie catch, as 1.2 per cent. Beard (1926) gives the phosphorus content of fish ash as 17.8 per cent. Therefore approximately 28.7 metric tons of phosphorus are removed yearly in the form of fish. This is equivalent to 6.3 per cent of the (minimum) assumed addition to the lake.

Approximately 25 per cent of the total yearly addition of phosphate phosphorus has been accounted for by chemical precipitation or biological removal. This does not include a variable amount removed by the growth of phytoplankton. A calculation may be made of the maximum amount removed at any one time by measuring the standing crop. Verduin (1951b) calculated the average standing crop to be 1.7×10^{23} μ^3 at the time of maximum population density in 1949. His estimate of the ash-free

[2] Verduin (1951a) showed that heterogeneity of turbidity in the vertical plane is a routine occurrence in the region of the Bass Islands. Chandler (1942) demonstrated the prevalence of this condition during 1940.

dry-weight of these diatoms is clearly in error, because his estimates show approximately 30 per cent of the wet weight would be organic matter, whereas even 10 per cent would be unusually high. Harris and Riley (1956) give 6.6 per cent of the wet weight of marine phytoplankton as organic matter, and my own measurements for freshwater and marine phytoplankton average 5 per cent. If the density of the diatom cells is taken as 1.1 and 5 per cent of the wet weight as organic matter, then 9.4×10^6 kg of organic matter was present, rather than 5×10^7 kg. Since one per cent of the organic matter of diatoms is phosphorus there were approximately 93.5 metric tons of phosphorus in the form of phytoplankton. Some of the plankton is carried out of the basin by currents, some is grazed by zooplankton which are in turn eaten by fish. There is regeneration of the element between each trophic level but this quantity cannot be assessed at the present state of our own knowledge. Since the plankton crop fluctuates from year to year and season to season, it must be regarded as a temporary phosphorus bank. A more permanent reservoir probably is the fish population. Although such factors as sediment accumulation have not been assessed, it appears likely that phosphorus loss from the western basin must be divided principally between sedimentation and outflow into the central basin. The former avenue of loss is most likely the major one.

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The Summer Standing Crop of Fish on a Shallow Bermuda Reef[1]

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ABSTRACT

Repeated estimates of reef fishes by visual counts were made on a shallow isolated Bermuda reef with a surface of approximately one hectare (2.5 acres). A standing crop of 490 kg was found in midsummer.

Comparisons between the fish fauna of this reef and more extended reef areas indicate that carnivorous reef fishes predominate on isolated reefs, while herbivores become more prevalent on large browsing areas. Available information on the yearly growth rates of Bermuda reef fishes suggests a relatively high overall efficiency of utilization of incident solar energy (*ca.* 0.0014%). The similarity of isolated reefs to ponds is discussed.

Estimates of standing fish crops have been used as indices of fertility of aquatic environments (Carlander 1955). From them alone, unfortunately, one can obtain only fragmentary information on the productivity of an area, but studies of rates of production may not be feasible especially if the region involved is poorly accessible. For this reason biological investigations of reef fishes are, as yet, mostly confined to the realm of taxonomy; reefs, after all, are in the tropics, fairly remote from the concentrations of aquatic biologists in America and Europe. The study of Odum and Odum (1955) is one notable exception; here the entire trophic structure of a Pacific reef was investigated, albeit in a relatively short time.

The aims of the present study were to make repeated estimates of the standing fish crop on a shallow Bermuda reef and to compare this isolated reef with more extended reef areas. Growth studies on certain species of reef fishes and observations on their movements were made in the same reef area (Bardach and Menzel 1957, Bardach 1958). Though these have been reported elsewhere they will be drawn upon in the discussion.

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MATERIALS AND METHODS

The study reef is located in Bermuda's northern reef chain, about 8 miles from the islands and almost 2 miles in a landward direction from the drop-off into the Atlantic Ocean (Fig. 1). It is part of a group of isolated reefs, rising from the lagoon floor at 40–50 feet almost to the water level. Waves do not break over it, but at low tide some of its coral heads are only two feet below the surface. It is irregularly oval, and dotted with smaller and larger sandholes which are between 15 and 20 feet deep and make up about one-third of its surface area (Fig. 2). The surface and the fairly vertical walls comprise roughly 2.5 acres (close to one hectare). This reef was not fished by commercial fishermen.

The predominant corals are: *Porites astroides*, *Diploria labyrinthiformes*, *Millepora alcicornis*, and some *Agaricia* sp. Staghorn coral (*Acropora* sp.) is absent from the Bermuda reefs, where one of the most striking features is the profusion of sea rods and sea fans with *Rhipidogorgia flatbellum*, *Pleuxaura flexuosa*, and *Eunicea grandis* as the most prominent. Algae such as *Dictyota* sp., *Zonaria zonalis*, and *Sargassum* sp. are the predominant plants which grow in profusion on dead coral.

The method of estimating the numbers of fish resident on this reef was to count them with the help of SCUBA equipment, along the lines reported by Brock (1954). Counts were made in August of 1955, 1956, and 1957.

FIG. 1. Map of Bermuda islands and surrounding reefs. *A*. Location of one hectare study reef. *B*. Location of study area on extended reef surface.

FIG. 2. Map of one-hectare study reef. The dotted areas represent sandholes.

The reef surface was divided into six to eight lanes by means of discarded telephone cable laid from a boat. The 1955 count was made on half the reef on each of two successive days; in 1956 eight divers were available and the entire reef was covered; in 1957 a scarcity of divers restricted the count to somewhat less than half the reef surface. All divers knew the local fauna. They were given opaque plastic slates with lists of the species they might expect to encounter so that they only had to make one pencil stroke for each fish. They started simultaneously and tried to keep abreast of one another. The counts on the vertical walls were made by two divers in all 3 years. They started from the same place and circled the reef in opposite direc-

tions. Thus, they checked each other's counts, as much as possible.

Tagging and recapture data for several species are available but were not included in the tabulation of the counts (Table 1) for reasons which will be given in the discussion. An estimate of nocturnal and crepuscular fish was made by rotenone treatment of a smaller area on an adjacent, very similar reef. Small fishes were counted on 100-m^2 quadrats, representing coral as well as sandy substrates.

In 1957 four lanes similar to those described above were laid on an extensive reef area near the edge of the reef barrier (Fig. 1); they comprised somewhat less than half an acre. Between June 14 and July 16 four counts were made by two divers at irregular intervals. Two additional counts by one diver extended the period of observation in this area to September 6, 1957. The two divers started at opposite corners of this area and each covered the entire four lanes after meeting the other in the middle. They thus arrived at two independent tallies of the representatives of certain selected species (Table 2). It was hoped that this additional survey might serve 1) to check on the reliability of the census method, 2) to yield some data to compare extended with isolated reefs, and 3) to indicate what day-to-day differences one might expect in the numbers of certain fish on the reef. The days on which these counts were made were largely determined by the weather.

Diving observations were also made during the winter of 1956 but no counts were attempted then. Average weights of the various fishes (Table 1) were based on length/weight tabulations from specimens secured by trapping and angling on surrounding reefs; several hundred fish were tabulated for some species, but at least 20 individuals were available for the rarer kinds. The modes in length-frequency distribution were used to determine average weights.

RESULTS AND DISCUSSION

Before discussing the results of the counts and their implications, an examination of the method and its reliability may be in order. Estimates of mixed marine fish populations by any method are difficult, and visual counts are possible only in clear tropical waters. It is of additional advantage for counting that most coral reef fishes are demersal.

Netting is not possible because of the irregularities of the substrate; baited traps may attract fish which do not "belong" on the reef, and on most days baited and unbaited traps failed entirely to catch certain species, or if an occasional catch was made, it was found unrepresentative of the numbers assessed by underwater counts (*e.g.*, grey snappers and grunts). Conversely it is possible that certain fish such as angelfish and groupers select a trap for their home (Bardach 1958), and this somewhat complicates the use of the marking and recapture method for population estimates on reefs. For these reasons trapping data have been omitted from the tables.

The use of fish poisons was found difficult on areas larger than half an acre, and even there many fish were known to have escaped in spite of previously set surrounding seines. Other fish were affected by the poison and were later found dead on the sandy bottom 500 yards or further from the poisoning site. Obviously, they could not all be collected by skin divers even with SCUBA equipment. In spite of these shortcomings there was no other method to estimate nocturnally active species which were hiding during the day. This estimate is suspected to be low unless one can assume that all nocturnal fishes left their hiding places under rotenone stress.

Dynamiting a portion of a reef might be another method to obtain a fairly complete sample. This, again was not a satisfactory method for several reasons: 1) the charge required for about half an acre of reef would have been awkward to handle adequately from the boat with shallow draft which we had to use, 2) it was not advisable for reasons of public relations, and 3) when dynamiting was tried on a small scale the sharks which were attracted made the collection of dead fish by swimmers and divers hazardous, if not impossible.

This clearly indicates that visual counts were, under the prevailing conditions, the least biased and best census method. It

TABLE 1. *Summer standing fish crop on a 1-hectare reef near Bermuda*

Fishes[1]	Numbers of individuals (and their estimated total weight, in kg)						Av. wt. kg/ha
	1955		1956		1957		
	No.	Wt.	No.	Wt.	No.	Wt.	
Omnivores (mostly herbivorous)							
Angelfish							
Holacanthus bermudensis (250)	82	20.5	47	11.8	45	11.3	14.5
Surgeonfish							
Acanthurus sp. (200)	150	30.8	27	5.4	18	3.6	13.3
Parrotfishes							
Adult *Scarus* and *Sparisoma* sp. (1000)	46	46.0	46	46.0	50	50.0	47.3
Subtotals, omnivores[2]		97.3		63.2		64.9	
Juvenile *Scarus* and *Sparisoma* (350)	70	24.5	—	—	—	—	24.5
Misc. small fish							
Young surgeon and parrotfish pomacentrids, etc. (10)	7000	70.0	4200	42.0	—	—	56.0
Total weight, omnivores							155.6
Carnivores							
Red hind							
Epinephelus guttatus (600)	63	37.8	24	14.4	42	25.2	25.8
Nassau grouper							
Epinephelus striatus (1115)	9	10.0	9	10.0	12	13.4	11.3
Other groupers							
Mycteroperca sp. (1500)	12	18.0	10	15.0	12	18.0	16.0
Coney							
Cephalopholis fulvus (400)	15	6.0	3	1.2	3	1.2	2.8
Grey snapper							
Lutjanus griseus (1000)	82	82.0	78	78.0	81	81.0	80.3
Bluestriped grunt							
Haemulon sciurus (400)	226	90.4	353	141.2	250	100.0	110.5
Porgy							
Calamus sp. (750)	3	2.3	1	0.8	6	4.5	2.5
Puddingwife							
Halichoeres radiatus (300)	4	1.2	2	0.6	1	0.3	0.7
Spanish hogfish							
Bodianus rufus (200)	24	4.8	15	3.0	25	5.0	4.3
Hogfish							
Lachnolaimus maximus (3000)	6	18.0	3	9.0	2	6.0	11.0
Subtotals, carnivores[2]		270.5		273.2		254.6	
Subtotals, omnivores and carnivores[3]		367.8		336.4		318.5	
Moray							
Gymnothorax sp. (400)	—	—	24	9.6	—	—	9.6
Small wrasses							
Thalassoma bifasciatum and *Halichoeres* sp. (10)	3200	32.0	4000	40.0	—	—	36.0

TABLE 1—*Concluded*

Fishes[1]	Numbers of individuals (and their estimated total weight, in kg)						Av. wt. kg/ha
	1955		1956		1957		
	No.	Wt.	No.	Wt.	No.	Wt.	
Small nocturnal and crepuscular fishes *Holocentrus* sp., *Apogon* sp. *Blenniidae* etc. (20)	—	—	1200	24.0	—	—	24.0
Total weight carnivores							334.8
Grand total weight							490.4

[1] Figures in brackets under species names give average individual weights of fish in grams.
[2] Subtotals of omnivore or carnivore species respectively for which three separate counts were made.
[3] Subtotals of all species for which three separate counts were made.

TABLE 2. *Occurrence of certain species of reef fishes on an extended reef near Bermuda, summer 1957, as counted by two divers, M and B*

Fishes	Date of Count									
	June 14		June 20		June 26		July 16		Aug. 19	Sept. 6
	M	B	M	B	M	B	M	B	M	M
Omnivores										
Parrotfishes										
Scarus	9	9	13	15	23	23	29	35	47	39
Sparisoma	9	6	27	12	33	19	28	20	27	22
Angelfish										
Holacanthus	—	—	14	15	14	14	18	19	25	20
Surgeon fish										
Acanthurus	11	4	30	21	20	14	21	18	33	28
Carnivores										
Red Hind										
Epinephelus guttatus	—	—	—	1	2	2	1	1	—	1
Groupers										
Mycteroperca sp.	—	—	—	1	—	1	—	1	—	—
Coney										
Cephalopholis fulvus	—	—	2	—	—	5	1	1	3	2
Grunts										
Haemulon sp.	3	3	1	2	4	2	5	5	2	4
Grey snappers										
Lutjanus griseus	3	—	—	1	—	—	—	—	—	—
Puddingwife										
Halichoeres radiatus	2	—	2	2	2	2	2	3	—	—
Others	—	—	9	7	5 (Barracuda)	4	3 (School of jacks, 50+, seen by both)	3	3	9

is quite likely that some fish were counted twice, in spite of instructions to divers only to count the fish in their own lane, but on the other hand it is equally likely that a fair number of fish escaped detection altogether.

On adding the weight of all species for which estimates were made in three successive years, though this does not represent the total weight of fish present, we find the three subtotals to be 368, 336, and 319 kg/ha, respectively (Table 1). The differ-

ence between the highest and lowest of these is 50 kg or 13.4% of the largest subtotal. It is likely that the highest estimate of 368 kg in 1955 is the least representative because more baited traps were set on the study reef during this year than during the following two. Some of the groupers, especially (*Epinephelus guttatus*), have been found to remain on the same reef for one or even two to three years, while others of the same species move from reef to reef (Bardach 1958). It is these roaming, larger fish which would stay on a reef as long as they find well baited traps as an inducement. In 1955 there was also an unexpectedly high count of surgeonfish (*Acanthurus* sp.), which is discussed below.

Table 2 contains independent counts by two divers on a larger reef. Among the 28 paired observations of fish seen by both divers, the same numbers were counted on 11 occasions. In 11 other counts diver M saw more fish than diver B, while B observed more fish than M in the remaining 6 of the 28 paired counts. Nine other times only one diver saw the fish of a certain species. Mostly there were only one or two animals involved here, but once one diver missed 5 coneys. This particular discrepancy is easily explained because the fish in question habitually hide in crevices. On the whole individual differences in counts may well compensate one another if the divers are all equally proficient in the use of their gear.

There is some indication in Table 2 that the numbers of omnivores increased from June to September. The counts are spaced too far apart to rule out chance or hydrographic conditions as the causes for this increase, but it seems equally likely that it is due to recruitment, since June to September represents the most favorable period for fish reproduction and growth in Bermuda.

A total standing crop of nearly 500 kg/ha (Table 1) is high compared to demersal fish populations in more northern latitudes (Merriman and Warfel 1947, Harvey 1950). This is to be expected in view of the great sculpturing of the reef which extends the surface area, the inclusion of vertical walls in the counts, the great variety of species, and the high average temperatures (the winter low for one or, at best, two months is 18°C, the summer high 28°C). On the other hand the standing crop estimate of this shallow Bermuda reef is of very similar magnitude to that from Eniwetok Atoll (Odum and Odum 1955), the only other comparable study in the coral reef environment. Values from their "zone D; complex larger heads" (considered similar to the Bermuda study area in the general configuration of corals and types of fish) showed that 93 kg/ha of the population was made up of herbivorous and 18.4 kg/ha of carnivorous fishes. These values are in terms of dry biomass. Assuming that water makes up 75% of the weight of fish (Vinogradov 1953) it is estimated that the total standing crop was 446 kg/ha. The Bermuda figure including the grunts and snappers, two species to be discussed later, is 490 kg/ha, a close correspondence indeed.

For purpose of analysis the fish listed in Table 1 were divided into omnivorous and carnivorous species. Those classified as omnivorous include some which are predominantly herbivorous such as the parrotfishes and the surgeonfishes. These contribute the largest weight of omnivores. Diving in February 1956 established that most large parrotfish were then absent from shallow reefs. It is presumed that they migrated into deeper water with the onset of winter conditions. A summer census may, therefore, give a misleading index of their true place in the annual economy of the reef. Surgeonfish and angelfish on the other hand are permanent residents of the shallow areas. The greatest discrepancy in the numbers of a single species occurred among the surgeonfish: 154 adult surgeonfish were counted in 1955, while only 27 and 18, respectively, were seen in the two subsequent years. Surgeonfish travel in schools of varying sizes, schools of 50 or more having been observed on large unbroken reefs. Large schools occasionally also cover greater distances than the largest extent of the study reef, possibly in consequence of their browsing habits. The high incidence of surgeonfish in 1955 is probably due to the visit of one or two large travelling schools, and the lower numbers of subsequent years come closer to the reef's carrying capacity for this species.

A comparison between larger reef areas and the study reef (Omnivores in Tables 1 and 2) suggests that the largely herbivorous omnivores are abundant on extended reefs and poorly represented on isolated ones. On the large reef they outweigh the carnivores about nine to one, while in the isolated area the weight of the carnivores is slightly less than twice that of the omnivores. This, at first glance, contradicts the classical concept of biomass pyramids, but there are several explanations for this discrepancy. 1) The numbers and the weight only of fishes were estimated. The largest fraction of herbivorous reef animals is probably mollusks, crustaceans, and annelids. These organisms are also the greatest source of food for carnivorous fishes. Carnivorous fish rarely feed upon omnivorous ones: no angelfish or surgeonfish were found in the stomachs of carnivores, and young parrotfish were only rarely ingested. 2) The largest numbers per species and also the largest weight was found among the grunts and snappers. These two species appear to feed only rarely during the day while they remain on the reef. They are reported to disperse at night and feed in the surrounding sandy area (Longley and Hildebrand 1941). The populations of these two species, characteristic as they are of the several isolated reefs which were checked, consisted entirely of adults and were present throughout the year. It seems likely that these species live on isolated reefs because they find many excellent hiding places on the vertical reef walls. Small grunts and snappers are very abundant in inshore waters but were seldom seen on the study reef. These observations suggest that it might be misleading to consider an isolated reef without, to some extent, also including the surrounding sandy areas. 3) Parrotfish swim over larger areas than that of the study reef and may require larger feeding ranges than can be provided by a one-hectare reef.

It is difficult to subdivide carnivores on the basis of predominant organisms in their stomachs, but some food analyses and a look at the dentition of certain fishes suggest, for instance, that the groupers, with a subtotal weight of approximately 50 kg/hectare, feed predominantly on crustacea and fish. The large wrasses and porgies (*Halichoeres radiatus*, *Bodianus rufus*, *Lachnolaimus maximus*, and *Calamus* sp.), representing ca. 20 kg/ha, feed mostly on mollusks.

Among the smaller fishes—excluding the young parrot and surgeonfish which are herbivorous—the ubiquitous pomacentrids, small wrasses, and butterflyfish feed on all kinds of invertebrates. Plant material is also often eaten, but it is not known whether this is accidentally or purposely ingested. The study of Menzel[2] on the Bermuda angelfish, a member of the butterflyfish family, suggests that these fishes cannot grow on plant material alone.

Pomacentrids are highly territorial animals which defend the areas around their attached eggs. They are the only fish on the reef that show these behavior traits to a marked extent. They are also the only reef fishes that are definitely known to have demersal eggs. Grouper and parrotfish eggs were found to be minute, present in large numbers per female, and to bear oil inclusions, which are some clues to a pelagic larval period. In the case of two species of groupers planktonic larvae have developed into juvenile stages in laboratory tanks. While pelagic eggs and larvae are common to many reef animals (Boden 1952), finding them among non-territorial reef fishes and not among territorial ones suggests that reproductive morphology and physiology had influenced the evolution of the inherited behavior pattern of territoriality, which in turn has been postulated to serve as regulator of population density.

The absence of an active defense pattern against intruders among the larger reef fishes such as the groupers suggests further that their numbers may be limited directly by the food supply. This is, to some extent, borne out by feeding experiments which were undertaken in a study of the growth of certain commercially important reef fishes (Bardach and Menzel 1957). Adult red hinds (*Epinephelus guttatus*), the most frequently found groupers on the shallow reef, increased to 300 % of their initial weight

[2] Menzel, D. W. 1958. Utilization of algae for growth by the angelfish (*Holacanthus bermudensis*). MS.

per year when fed to satiation in laboratory holding tanks. The feeding periods from which these figures were prorated lasted only 20 days, and one could expect the food intake to level off if the experiments had been prolonged. The fish also certainly moved less in the tanks than in the natural environment. In spite of these cautions, some reef fishes seem to possess an unrealized growth potential which may, in part, be explained by a limitation of the natural food supply.

The yearly growth rates of some species on the reef were determined by recaptures of tagged fish (Bardach and Menzel 1957). Juvenile and adult carnivorous groupers added between 30 and 40% of their body weight per year allowing for slower growth during the winter; the figure for the omnivorous adult angelfish is 32%. The growth rates of the other species—grunts, snappers, and parrotfishes as well as all young of the year—are not known. It is also not known what percentage of the larger parrotfishes spend the winter in deeper water.

No commercial fishing occurred on the reef where three independent yearly estimates of the summer standing crop gave consistent results. We may, therefore, assume that growth and immigration roughly balanced natural mortality and emigration. With these cautions in mind certain speculations may now be advanced.

It is in keeping with the assumptions of similar studies and the indications gained from our own to estimate that the reef fish biota grew in weight at a rate of about 35% per year, although this value seems low when compared to the growth rates of fish in Block Island Sound (Riley 1955) and the English Channel (Harvey 1950). The absence of commercial fishing on the reef might counteract the effect of long seasonal growth favored by Bermuda's water temperatures, and a greater proportion of large, slowly growing individuals might, therefore, have occurred here than in areas of intensive commercial fisheries. Also certain fish are not on the study reef during the winter months. Their weight increment while absent would tend to lower the yearly overall growth figures. On the other hand, almost a fourth of the standing crop is made up of small, presumably shortlived fishes which do not leave the reef (Bardach 1958) and of young of the year. They can be expected to grow by more than 35% per annum. However, in the absence of more detailed growth data a 35% yearly overall growth is suggested as a first approximation.

At this rate the total yearly growth amounts to 172 kg/ha (35% of 490 kg). Homogenized whole reef fish have an energy value of 1.3 Cal/g, (determined by calorimetric procedure) and the assumed growth, therefore, represents the fixation of 2.2×10^5 Cal/ha/year. The average incident radiation in Bermuda has been estimated at 1.6×10^{10} Cal/ha/year (U. S. Weather Bureau 1954). The overall efficiency with which fish (mostly tertiary consumers) utilized solar energy on Bermuda reefs therefore approximated 0.0014 per cent. Inaccurate as this estimate may be because of the cautions advanced above, this figure is considerably higher than the efficiency estimates (0.00005 to 0.00025 per cent) for George's Bank obtained by Clarke in 1946. His values were based on commercial landings and not on growth, and it was estimated that these landings may represent the removal of 50% of the yearly production of marketable fish. But even on doubling Clarke's upper figure the overall efficiency of conversion of solar energy into fish flesh still appears to be about three times that of George's Bank.

Hayne and Ball (1956) in comparing solar radiation with fish production in a shallow pond in Michigan (average depth 3 feet) arrived at an overall efficiency value of 0.0014 per cent. Bennett (1943) and Carlander (1953) quote standing crop estimates of 400 to 500 pounds per acre as common in Illinois and Iowa ponds with mixed fish populations; much of this weight is made up of young of the year, and overall efficiency values of utilization of incident energy are probably also high. These bodies of water are freshwater environments, more self-contained than the reef, but they are also shallow. The close correspondence between efficiency estimates from pond and reef suggests that high utilization of incident radiation by tertiary consumers may be

typical of shallow waters where a substantial amount of solar energy reaches the bottom.

Silver Springs, Florida, is another example of a shallow aquatic environment with high plant productivity (Odum 1957). While it is not possible to make numerical comparisons on the fish level, the ratio between incident radiation and fish productivity indicates a high overall efficiency here also.

The Bermuda coral reefs are located in the Sargasso Sea which is renowned for its infertility, but the relative fertility of the reefs themselves is high. Reefs are littoral areas where attached primary producers abound. Nutrients may be retained there for at least part of the year (Boden 1952), and the utilization of solar energy by attached and symbiotic reef algae is as high as 3 per cent (Odum and Odum 1955). Sargent and Austin (1954) showed that Rongelap atoll was a self-sufficient community with a productivity per unit area that was considerably higher than that of the adjacent waters. This supports the belief that a high overall productivity is also a characteristic of Bermuda reef areas.

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Effect of Water Clarity on Albacore Catches

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ABSTRACT

The numbers of albacore (*Germo alalunga*) taken by gill-netting and surface trolling are seriously affected by the transparency of the water. Observations assembled from a fishing cruise between Hawaii and the Aleutians in 1956 and from a cruise off the Pacific coast of North America in 1957 showed that the efficiency of the troll was greater in clear water than in more turbid water. Very likely this increase in efficiency is a power function of the change in transparency. Though the data are not so convincing, the results suggested that the gill net fishes more efficiently in turbid water. The ratio of troll catch to gill-net catch bears the following relation to a reciprocal function of the extinction coefficient—

$$\frac{\text{Troll} \times 100}{\text{Gill net}} = .0000394 \left(\frac{1.7}{\text{Extinction coefficient}} \right)^{4.55}$$

Since the theoretical maximum power function of the troll catches alone is about 3, the residual of 1.55 may be associated with the reverse effect that water clarity has on the efficiency of the gill net.

These data are discussed in relation to evaluating the abundance of any species of fish when the method of assessment involves visual responses. In addition, the possibility is discussed that water clarity may be an important ecological factor in the ocean in that the efficiency of sight feeders will be reduced as turbidity increases.

INTRODUCTION

Students of the ocean have long recognized that water clarity is an important ecological variable through its effect on photosynthesis (Clarke 1939) and on the maximum depth at which organisms might be able to see (Clarke 1936). Tamura (1957) and other investigators have concerned themselves with the morphology and histology of fish eyes and with measurements of the thresholds of vision in terms of illumination and of the most efficient level of illumination for vision (Tamura *et al.* 1957). Finally, in recent years there has been considerable attention devoted to variation in the optical properties of ocean water with depth (Jerlov 1951). Our concern is with a slightly different aspect of the problem. We wish to consider how far a fish can see in its normal habitat (a quantity similar to visual range as defined by Jenkins and Bowen 1946), and its effect on distribution and sampling of the fish.

In 1955 the writer hypothesized that the clarity of oceanic waters may have a direct influence on the abundance and distribution of tunas through its effect on their ability to forage. The hypothesis seemed to have merit, and observations and preliminary investigations pertinent to the problem were initiated shortly thereafter. A study of the morphology and histology of tuna eyes was begun under contract at the University of Hawaii, and we began measuring water clarity in connection with fishing surveys insofar as instrumentation and time permitted.

The material to be presented here does not permit direct discussion of the primary hypothesis. Rather, it shows that methods of catching tuna that depend on visual response of the fish are efficient in proportion to the clarity of the waters—by implication supporting the original hypothesis. The evidence shows that trolling, which depends on a positive visual response, is most efficient in clear water, whereas gill-netting, which is dependent on non-response, is most efficient in turbid water.

MATERIALS AND METHODS

The data utilized in this study were collected during the course of two albacore

(*Germo alalunga*) fishing surveys. The first survey was conducted in the summer of 1956 in temperate waters lying between Hawaii and the Aleutian Islands. The second survey was made during the summer of 1957 in the waters off the west coast of the United States. For the purposes of this study pertinent observations were grouped into synthetic stations. These are centered on overnight gill-net sets, and also include trolling during the afternoon preceding and the morning following the gill-net sets. Daylight extinction measurements were made near mid-day before and after the gill-net sets.

Daylight extinction was measured by determining the depth at which 5 per cent and 10 per cent of the surface illumination persisted. The apparatus consisted of a deck cell, mounted on gimbals and containing a Weston Photronic Model 856 type 1 photoelectric cell, and a similar submerged cell, each equipped with a suitable filter to match its response to the standard luminosity curve adopted by the International Commission on Illumination. A microammeter completed the apparatus. Determinations were made by placing an appropriate calibrated cover over the deck cell and lowering the sea cell until its current output equalled that of the deck cell. The two determinations (5 and 10 per cent) were coverted to extinction coefficients (Sverdrup *et al.* 1942, p. 82), and the two extinction coefficients were averaged. As might be expected from the differential extinction of different wave lengths of light through a water column and the possibility of heterogeneity of the water columns, the two coefficients (5 and 10 per cent) were not identical, but they generally bore a linear relation to one another and to the average of the two, suggesting that the average coefficient is a useful relative measure of transparency.

A final problem with respect to the extinction coefficients was to derive a value for each synthetic station that would be representative of clarity during trolling and gill-netting. Since ordinarily the ship moved 10–60 miles from one noon to the other, that is, from one light measurement to the next, there were no transparency observations directly associated with the gill-netting. Though somewhat unsatisfactory, our method of solving the difficulty was to average the two noon values of clarity bracketing the fishing, on the assumption that transparency varied linearly between stations. The light penetration measurements when plotted on surface charts to check this assumption indicated that, by and large, transparency varied in a progressive manner over a noon-to-noon vessel track. In three instances additional values obtained two or three days before or after a synthetic station were included because they fell on the vessel track. Thus each extinction coefficient employed here usually is the mean of four field determinations: two (5 and 10 per cent) at the noon preceding the fishing effort; and two (5 and 10 per cent) at the noon immediately following the fishing effort. It should be noted that the most turbid water encountered corresponded roughly to the oceanic maximum recognized by Sverdrup *et al.* (1942, p. 85) and that none would fall in the category of coastal water with respect to turbidity.

Trolling was generally carried out with the vessel proceeding at 5–7 knots, trailing 5 or 6 lines. These lines bore a variety of "albacore lures," and there was no indication from the catch that one lure was superior to the others. No adjustments were made in the raw troll catches except for one station during which there was no trolling on the morning following the gill-net station. In that instance the troll catch of the afternoon preceding the gill-net station was arbitrarily doubled.

The albacore gill nets were made up of shackles about 300 feet long and 30 feet deep, with mesh size ranging from 4½ to 7½ inches (stretched measure). Between 9 and 18 shackles were fished at each station, 12 being the typical number. Since all mesh sizes took albacore, we have made no attempt to adjust the catch for varying proportions of the different mesh sizes. Rather, the results are expressed in terms of catch per 12 shackles of net. Gill nets were set at dusk and hauled just prior to dawn.

Approximately 35 sets of fish-catch and transparency measurements were available

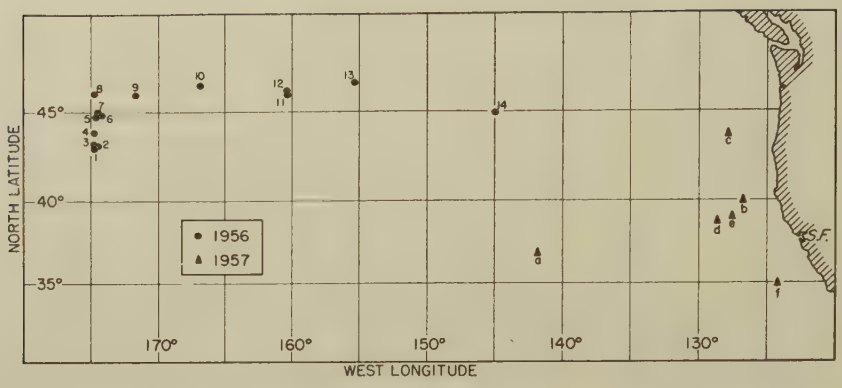

FIG. 1. Northeastern Pacific Ocean, showing the locations of troll and gill-net stations used in this study. The July-August 1956 cruise is represented by solid circles and the June-August 1957 cruise by triangles.

TABLE 1. *Albacore catches and mean extinction coefficients during 1956 and 1957*

Dates and positions refer to the start of the gill-net stations. Gill-net catches are adjusted to 12 shackles. Troll catches are from noon to noon bracketing the gill-net stations. Extinction coefficients are the means of the 10 and 5 per cent determinations of all light stations during the noon-to-noon periods.

Station	Date	Latitude	Longitude	Gill-net catch	Troll catch	Extinction coefficient
1	7–25–56	43° 02′ N	174° 57′ W	27	5	.119
2	7–26–56	43° 07′ N	174° 52′ W	81	1	.137
3	7–27–56	43° 10′ N	174° 53′ W	33	1	.148
4	7–28–56	43° 56′ N	174° 57′ W	16	1	.157
5	7–31–56	44° 48′ N	174° 46′ W	112	11	.086
6	8–1–56	44° 54′ N	174° 08′ W	32	11	.090
7	8–2–56	44° 58′ N	174° 29′ W	33	6	.094
8	8–3–56	46° 01′ N	174° 58′ W	16	0	.089
9	8–16–56	45° 57′ N	171° 44′ W	53	4	.095
10	8–19–56	46° 28′ N	166° 54′ W	33	3	.130
11	8–21–56	46° 00′ N	160° 16′ W	63	0	.130
12	8–22–56	46° 03′ N	160° 16′ W	79	0	.149
13	8–26–56	46° 25′ N	155° 15′ W	13	0	.116
14	9–1–56	44° 57′ N	145° 01′ W	4	7	.106
a	6–19–57	36° 53′ N	141° 41′ W	27	4	.052
b	7–9–57	39° 59′ N	126° 51′ W	3	12	.063
c	7–23–57	43° 42′ N	127° 53′ W	11	12	.072
d	7–28–57	38° 45′ N	128° 37′ W	2	15	.055
e	7–29–57	39° 00′ N	127° 31′ W	28	6	.074
f	8–9–57	34° 50′ N	124° 10′ W	2	13	.071

for study. These were reduced to 20 by considering only those stations in which the aggregate catch of the gill-net set and the trolling was 10 or more fish. This limitation reduced the variability in the data and, perhaps even more important, restricted the study to waters in which albacore were present in fair numbers. Thus, the problem of the general distribution of albacore and the possible interaction of other environmental factors on the catches, such as temperature, is minimized. The locations of the 20 stations that met the above criterion are shown in Figure 1 and the data are tabulated in Table 1.

RESULTS

The results of gill-netting show little numerical relation to the troll catches (Fig. 2). Though far below the level of statistical significance, the two have a negative correlation coefficient as would be expected if they are affected in opposite ways by water clarity. Statistically significant results should not be expected, however, without enormous amounts of data, because the treatment does not overcome variations in the absolute abundance of albacore from station to station; and since two measures of abundance are plotted, this effect is doubled.

Troll catches, plotted as a function of water clarity (extinction coefficient), show a negative relation ($r = -0.738$, $P < 0.01$) (Fig. 3). A linear function was applied, not because it is proposed that the two variables bear a linear relation to each other, but rather as a simple way to show that there is an association between them. Again, an unknown source of variability in this treatment must be the changes in the true abundance of albacore from station to station. However, the effect of this source of variability is less than in the previous analy-

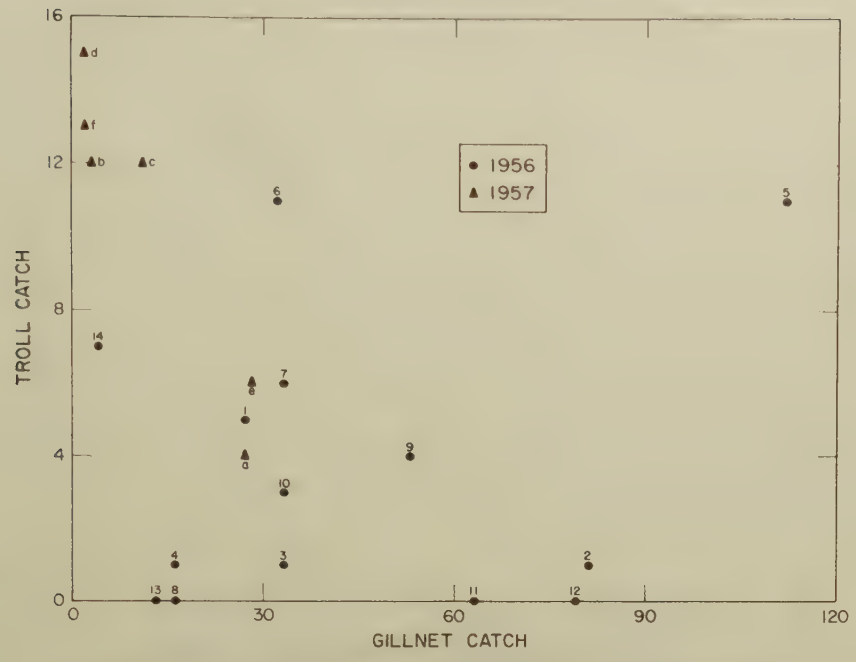

FIG. 2. Troll catch of albacore, plotted against the gill-net catch.

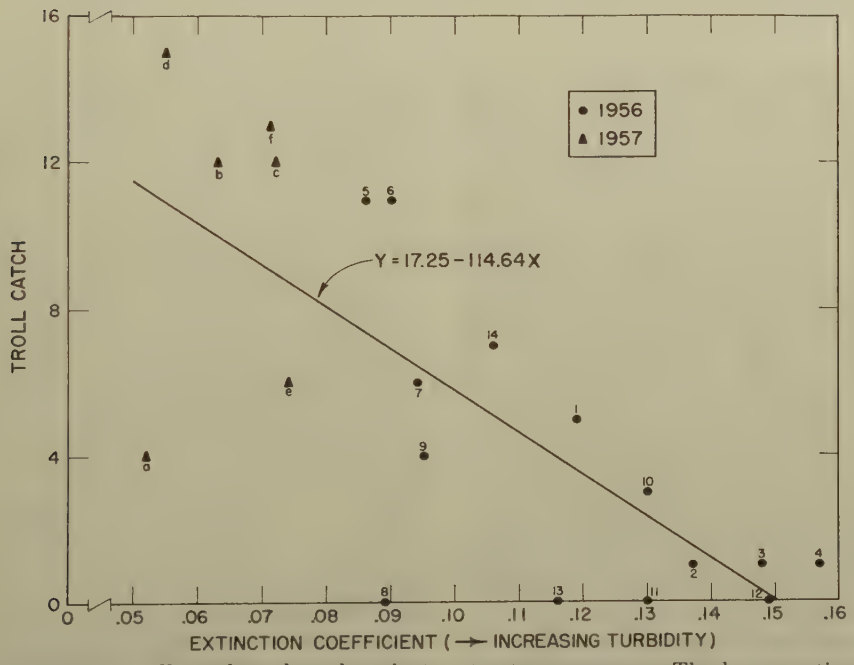

FIG. 3. Albacore troll catches plotted against water transparency. The larger extinction coefficients represent less transparent water.

sis because we consider only one measurement of the albacore population. Figure 3 could, of course, be interpreted to mean that albacore are most abundant in clear water or that trolling is most effective in clear water or, as a third possibility, there may be an interaction or systematic effect of the different variables.

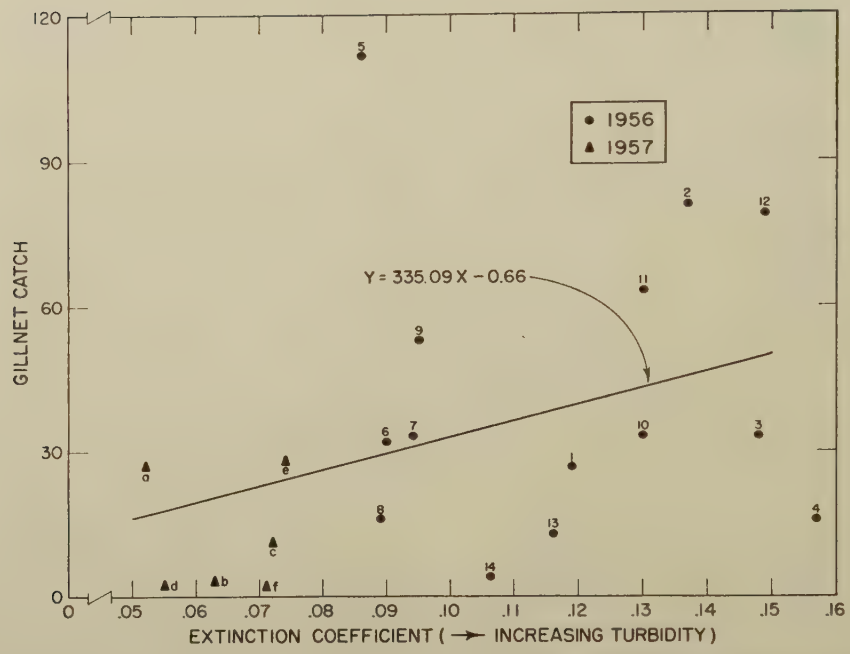

FIG. 4. Albacore gill-net catches plotted against water transparency. The larger extinction coefficients represent less transparent water.

Gill-net catches plotted against turbidity show a positive relation ($r = 0.36$, $P > 0.05$) (Fig. 4). Lack of statistical significance may well stem from the ever-present variability associated with differences in the actual density of the albacore population and the tendency for night gill-netting to reduce or perhaps even eliminate the effect of variations in water clarity. Auxiliary sources of light must also be considered with respect to the gill net. Extremely clear water is generally low in biomass and probably would produce little bioluminescence in the vicinity of the drifting gill net. Turbid water in the marine environment is generally high in biomass and might therefore result in high bioluminescence. This additional variable would operate to reduce the slope of the regression.

If we accept the slope in Figure 4, we are again offered three alternate conclusions: (1) that albacore are more abundant in more turbid water, (2) that the gill net fishes more efficiently in more turbid water, or (3) that there is systematic interaction among the variables. These are opposite to the conclusions drawn from the troll catches. If the slope, which falls slightly short of significance, is rejected in compliance with the usual statistical standards, we can conclude that the magnitude of the gill-net catch and presumably the density of the albacore population is independent of water clarity.

The preceding analyses of water clarity and albacore catches were handicapped by inability to estimate or control variations in absolute abundance from station to station. One way to eliminate the effect of absolute abundance is to express the catches as a ratio (Troll catch ÷ Gill-net catch), adding "1" to the three zero catches in Table 1. If these ratios are plotted against water clarity, the slope obtained will be independent of abundance and should only reflect the relative efficiency of the two sampling methods with respect to water clarity. This treatment has the disadvantage of introducing into one analysis all sources of random variability, that is, variability in gill-net catches, troll catches, and random errors in assessing water clarity.

In this final analysis an approximation of

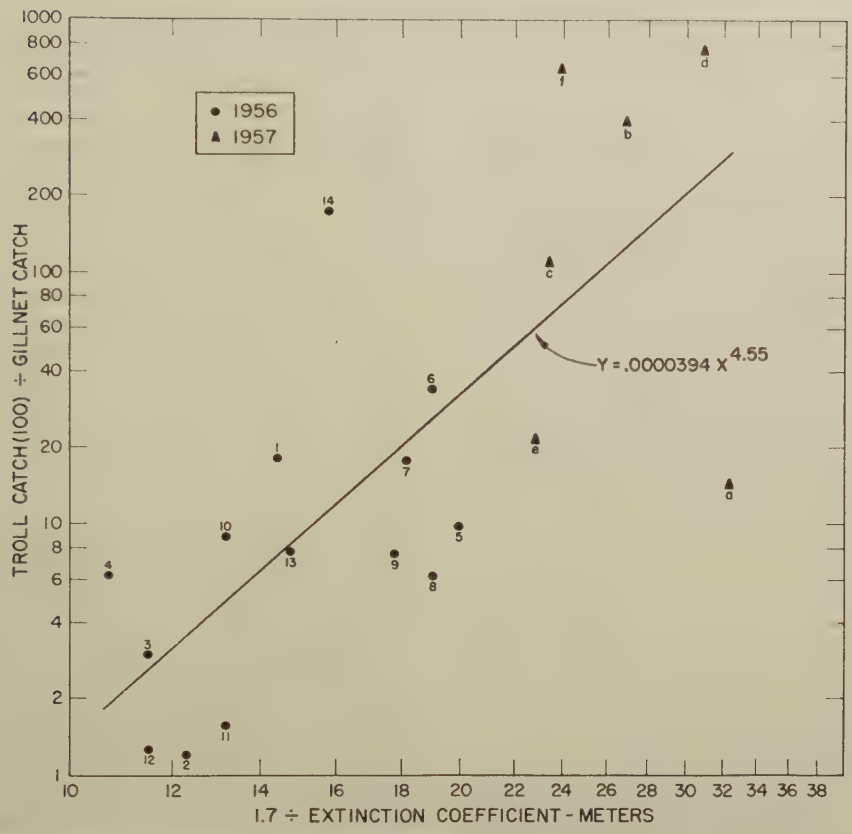

FIG. 5. The ratio of troll to gill-net catches plotted as a function of the reciprocal of the extinction coefficient.

the distance an albacore can see (visual range), *i.e.*, $\frac{1.7}{K}$ is employed as the measure of water clarity instead of the extinction coefficient (K). This reciprocal quantity of the extinction coefficient was found by Poole and Atkins (1929) to be equal to the vertical depth at which a Secchi disk could be seen in the English Channel. A comparison of our Secchi disk measurements and the computed $\frac{1.7}{K}$ indicates the latter is also a good approximation in these waters. (The observed Secchi disk measurements were not used in the present study because they lack the precision of the photoelectric determinations, principally because of variation in boundary conditions at the sea surface.)

The relative efficiency of the two sampling methods $\left(\frac{\text{Troll} \times 100}{\text{Gill net}}\right)$ is treated as a power function of the visual range $\left(\frac{1.7}{K}\right)$ because the efficiency of the troll should be related to some power of the radius of vision, that is, the visual range. Thus the following type of equation should obtain—

$$\frac{\text{Troll} \times 100}{\text{Gill net}} = a\left(\frac{1.7}{K}\right)^b$$

The empirical solution to the above equation (Fig. 5) gives a value of 3.95×10^{-5} for a and 4.55 for b. The slope is highly significant ($P < 0.001$) as is the associated correlation ($r = 0.772$). Again, as suggested by the other treatments, the efficiency of the troll in respect to the gill net is apparently a function of water clarity. This analysis tends to implicate the gill net as well as the troll, because the b value (4.55) is higher than might be expected if the gill net is unbiased with respect to water clarity. That is, if an instantaneous function is con-

sidered, the volume of water in which the troll lure is visible to albacore should be close to a cube function of the visual range because an object near the surface is visible to all fish in a "hemisphere," with locus at the object and a radius equal to the visual range.[1] No significantly higher exponent can be theorized, so most of the residual (1.55) must be either related to increasing gill-net efficiency with increasing turbidity or to sampling error or both.

DISCUSSION

The validity of using extinction coefficients (K) to estimate how far a fish can see is not clearly established. Poole and Atkins (1929) showed that in the English Channel $\frac{1.7}{K}$ was a linear function of the vertical limit of Secchi disk visibility. The present problem, however, involves vision at all angles from the horizontal to the vertical. We have made measurements comparing vertical and horizontal Secchi disk visibility at two locations in Hawaiian waters with the observer on a submerged platform about 4 feet below the sea surface. In each of two pairs of observations, one determination was made vertically and a second, with a similar target, horizontally, the target being suspended from a buoy about 10 feet below the surface. In each instance the vertical and horizontal determinations were nearly identical, varying about 10 feet (vertical distances 150 and 180 feet). Thus the vertical Secchi disk determinations appear to provide a fairly close approximation of horizontal visual range. Since this quantity is a function of the extinction coefficient it appears that the use of $\frac{1.7}{K}$ as a first approximation of visual range is justified. The basic reason for the validity of this approximation lies in fact that loss of contrast through scattering is the most important element in fixing "visual range" in the open ocean, with absolute level of initial illumination of minor importance (Duntley 1952).

Perhaps it is redundant to point out that the evidence given questions the validity of estimates of tuna abundance if the methods are such that the fish can employ vision in a positive or negative sense in relation to the gear. A case in point are Figures 3, 4, and 5 in which the data for 1957, while not incompatible with those obtained in 1956, are not randomly distributed with respect to the 1956 results. This apparently resulted because gill-net stations in 1957 were deliberately located in areas where trolling was "good," practically precluding a random distribution of gill-net catches with respect to water clarity. Comprehensive sampling programs employing two or more types of gear might help to overcome this problem, and more precise information on the magnitude of the effect of water clarity and other environmental factors on the efficiency of the sampling method might permit adjustment of catches to obtain a more reliable measure of actual abundance. Another alternative is to sample by means of measures not dependent on any reaction of the fish to visual stimuli. For instance, the gill net as used for albacore appears to be an improvement over the troll, though the gill net might be more susceptible to other factors such as the vertical distribution of fish and the thermal structure of the water. An ecologist attempting to relate abundance of, say, albacore to other factors in the environment might even better be served by the uncertain but unbiased estimates of fish abundance that might be obtained by echo sounders.

Though it is not possible to treat the subject with any precision, it is worthwhile to consider further the possible effect of water clarity on the absolute abundance of albacore and other sight feeders. The first problem, of course, is to establish that they are sight feeders. This is indicated with respect to

[1] The cube function is only an approximation because an object can be seen over the greatest range from directly below, and at a lesser distance from a horizontal direction (Duntley 1952). Thus the volume of water in which the lure is visible is an ellipsoidal solid with a vertical axis slightly greater than the horizontal. The present data do not permit precise resolution of the parameters involved, but trial computations show that no more than 0.2 of the 1.55 can be ascribed to deviations from a sphere.

albacore and other tunas by general observations on their behavior at sea and by such objective data as failure to make captures at night by trolling. It is also suggested by their large and presumably efficient eyes and by their ability to swim rapidly. Vision in the open ocean appears to be related to turbidity, which is of course related to the amount of particulate matter in the water. In the open ocean the amount of particulate matter is at least in part a function of the biomass; thus as the standing crop of food increases, the relative ability of the tunas to locate and capture a prey animal must decrease. Fish such as tuna might then be at a loss in an environment judged ideal on the basis of the standing crop of organisms. An extreme case of this effect might run as follows: A particular area contains a crop of tuna forage sufficient to support a particular density of tuna. An increase in the rate of replenishment of nutrients in that area through upwelling or some other phenomenon causes an upsurge of phytoplankton, thus decreasing the visibility. However, there might not yet be an increase in the tuna food supply so the tunas would be forced temporarily to desert this particular area. Perhaps this effect contributes to the reported exclusion of herring from dense populations of phytoplankton, for they also appear to employ vision in capturing food (Vilter 1950).

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1100–Meter Dive in the Bathyscaph *Trieste*

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ABSTRACT

This paper describes a dive made in the bathyscaph TRIESTE on July 3, 1957, with the writer as the scientific observer and Jaques Piccard as the pilot. This was the fifth dive of a series of twenty-eight dives made during 1957 and sponsored by the U. S. Office of Naval Research. The dive lasted 2 hours and 31 minutes, with 36 minutes spent on the bottom.

On July 3, 1957, the writer participated as the scientific observer in the 27th dive of the bathyscaph TRIESTE. This particular dive was to a depth of 1100 meters (3600 feet) in the Mediterranean Sea 1.9 miles south of the Isle of Capri at Latitude 40° 30′ 30″ N and Longitude 14° 13′ 00″ E. The pilot on this dive, as for all other dives of the TRIESTE, was Jacques Piccard, who has been in operational control of this privately owned deep-sea diving craft since its launching in 1952. This was the 5th dive of the 1957 diving season, the first having been a shallow test dive in the Bay of Naples with William Kielhorn (Office of Naval Research, Woods Hole). This was followed by three other dives to a maximum depth of 600 meters with Dr. Nils Jerlov (Oceanographic Institute, Göthenburg, Sweden) as the scientific observer for the purpose of measuring the penetration of sunlight and light scattering. Appropriately, the first scientific dive was made on 1 July, the opening day of the International Geophysical Year.

During the 1957 diving season a total of 26 dives was made, mostly to depths of about 1000 meters since waters this deep lie within easy towing range of Castellammare di Stabia where the TRIESTE was docked. However, one extended tow was made to the Isle of Ponza from where descents were made to 2800 meters, 3000 meters, and 3200 meters. The last of these was the deepest 1957 dive and was exceeded only by the TRIESTE's 1956 dive to 3700 meters in the center of the Tyrrhenian Sea. While at Ponza the TRIESTE also made a dive to 300 meters in 3000-meter-deep water and was suspended at this depth for four hours in connection with an acoustic experiment. This unusual performance demonstrated a unique experimental usefulness for bathyscaphs.

Most of these later dives were made by an American team of oceanographers and underwater sound specialists consisting of A. Rechnitzer (U. S. Navy Electronics Laboratory, San Diego, California), R. Lewis (U. S. Navy Underwater Sound Laboratory, New London, Conn.), M. Lomask (Hudson Laboratory, New York), Roberto Frassetto (Hudson Laboratory), Richard Vetter (Office of Naval Research), and A. Maxwell (Office of Naval Research). The entire 1957 TRIESTE program was made possible through a contract (No. N62558-1392) between the Office of Naval Research and J. Piccard to support the further development and scientific utilization of this bathyscaph. Also essential for the success of the dives was the assistance of the above named laboratories which provided personnel and equipment for scientific collaboration with Piccard.

Some of the American equipment which was then installed on the TRIESTE included the following: (1) an airplane-type magnetic compass which was compensated inside the cabin; (2) a two-way voice and cableless underwater telephone for maintaining contact between the TRIESTE and the escorting surface ship; (3) an exterior deep sea camera especially built for bathyscaph use by Pro-

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fessor Harold Edgerton of Massachusetts Institute of Technology; and (4) various oceanographic and biological sampling devices mostly built at the U. S. Navy Electronics Laboratory. However, at the time of my dive, only the compass had been installed. It also should be emphasized that the success of the dives depended upon the cooperation of the Italian Navy in providing a tugboat and other accessory craft, of the shipyard (Navalmeccanica at Castellammare di Stabia) for the use of its facilities, and of the petroleum company A.G.I.P., which loaned 28,000 gallons of gasoline for flotation. A summary account of the 1957 ONR TRIESTE diving results has already been published (Dietz *et al.* 1958). The TRIESTE has subsequently been transferred to San Diego, California, for further testing and diving at the U. S. Navy Electronics Laboratory.

Since the principle of a bathyscaph may be only vaguely known to some readers, a brief resumé follows. To understand how it functions, it is sufficient to consider the craft as the underwater analogy of a balloon or, even more exactly, a non-rigid lighter-than-air ship or "blimp." The craft has a compartmented flotation hull 15 m long which can hold 74 metric tons (106 m^3 or 28,000 U. S. gals) of gasoline. Assuming a density of 0.70, this provides a positive buoyancy of 32 tons. The hull is not designed to withstand the high hydrostatic pressure of the deep sea; instead, water is freely admitted to the hull through orifices at the bottom as the gasoline becomes compressed with depth or contracts owing to cooling. The gasoline, being immiscible and lighter than water, continuously floats on top of any water entering the hull.

A 10-ton forged steel spherical chamber is suspended below the hull. This measures 2 m inside diameter and 9 cm wall thickness (thickening to 15 cm near the portholes and door), in which the pilot and a scientific observer are housed. This cabin is made of two hemispheres which are clamped together—the high pressure seal being provided simply by a precision machined metal-to-metal contact. This high pressure cabin can withstand the pressure at 6000 m with a safety factor of 3. Hence, the TRIESTE is designed to reach about 99% of the sea floors of the world, being restricted only from the great trenches Entrance into the cabin is made by descending a vertical air lock of "sas" from topside and passing through a 43-cm-diameter door; the air lock is flooded during descent and blown out with compressed air upon surfacing. The cabin has both fore and aft wndows made of truncated cones of plexiglas 15 cm thick, 40 cm wide outside, and 10 cm wide inside. The cabin also contains 12 lead-throughs for the electric cables for operation of the craft and for navigational and scientific equipment, and two lead-throughs for snorkels to conserve oxygen in an emergency when "buttoned up" on the surface.

The craft is submerged by taking on water ballast in tanks at the two ends of the hull. Additional negative buoyancy when under water can be obtained by valving off a small quantity of gasoline. This jettisonable gasoline is entirely contained in the central compartment. And even if all of it is entirely replaced by sea water, there is sufficient additional buoyancy from the other tanks to permit the TRIESTE to return to the surface. The craft can be made to ascend at will by jettisoning some of the 10 tons of iron pellets contained in two fore and aft silos. The shot is held in the silos by an electromagnet which can be shorted by the pilot, or, if there is electrical failure, it will drop automatically. Horizontal maneuverability for short distances under water is accomplished through the separate or combined use of two propellers located topside which thrust the craft slowly forward or backward. For additional technical details the reader is referred to the book on the TRIESTE by A. Piccard (1956).

My dive commenced at 1515 and ended at 1746, a total elapsed time of 2 hours 31 minutes. It was the second dive of the day, following one to 600 m by Piccard and Nils Jerlov. The weather was sunny and the sea almost flat. The descent commenced when the topside crew flooded the air tanks and filled the entrance shaft with water. We had a little difficulty in getting the TRIESTE to sink immediately as she was rather lightly ballasted. First she settled to

about 25 meters where the seasonal thermocline was encountered; below this there was, of course, denser water. This interrupted the descent and, in fact, the craft rose to the surface. Some gasoline from the central compartment was then valved off enabling the descent to begin in earnest. No life was seen in the surface water except for two small medusae which drifted past the porthole. The water was beautifully blue and clear; the sun's rays could be seen dancing about. As we descended I looked intently through the porthole in the hope of visually detecting the thermocline. I thought that one might be able to see a turbid layer or some refraction effects due to mixing as we went through this abrupt temperature discontinuity, but in fact nothing was detected. There were, however, a moderate number of large scattering particles which were probably resting on the thermocline.

At D + 15, that is, 15 minutes after the dive began, we were only at a depth of 45 meters. Even at this depth any evidence of buffeting by surface waves, which had set up a rattle of loose bottles and other gear, had stopped so that we seemed perfectly stable. The cabin was warm and stuffy so we turned the oxygen bottles on. The oxygen in the air of the cabin normally lasts two occupants about an hour before new oxygen must be added.

By D + 25, at a depth of 160 meters, the light had become much dimmer—like the falling of evening. We were entering the ocean's twilight zone. Once the floodlights were turned on, it was possible to see numerous scattering particles rising past the porthole like an inverted, very light snowfall. By D + 35 we had reached a depth of 350 meters; we were now descending much faster. Piccard had valved off some more gasoline a little earlier; this plus cooling and the compressional contraction made the craft heavier. It was quite apparent by now that the number of scattering particles in the water was increasing with depth, and it could also be seen that many of these particles were living zooplankton rather than dead organic detritus. However, the descent was too fast to allow identification. The first flash of bioluminescence was noted at 350 meters. The temperature of the water was 16°C according to the cabin thermometer, or still 4°C warmer than the usual deep temperature of the Mediterranean Sea. The cabin was now quite cool and pleasant.

At 400 meters some steady rather than flashing "phosphorescence" was seen for the first time. A series of lights in a row was noted which may have been from some species of deep sea fish. However, such sights passed by the porthole too quickly for certain identification.

The writer was reminded of the very much better "seeing" he had enjoyed in 1952 when making a dive to 120 meters in the Japanese diving bell KUROSHIO. This descent was made very slowly and at times the bell was completely stationary. But more important, the observer was looking almost straight down a powerful light beam which made it possible to see easily zooplankton as small as copepods. In contrast the TRIESTE lights are placed well above the observer, forming an attenuated double cone of light which makes it difficult to discern anything except the larger zooplankton.

During the entire dive the floodlights were switched on and off. They were lit for only about ten seconds at a time, since they were already near the end of their short expected life. Piccard feared that they might burn out and spoil the remainder of the dive. These Philips-made mercury vapor lamps are one of the remarkable technical aspects of the TRIESTE. They are directly exposed to the sea water for cooling, and principally because of their minute size (about 2″ long and thinner than a pencil) they can withstand great hydrostatic pressure.

During the descent we carefully watched the fading of ambient sunlight. We wished to record the exact depth at which the abyssal zone of perpetual night was entered. The human eye, of course, is remarkably sensitive, being capable of discerning light when it is only about one ten-billionth part of full daylight. At 500 meters I could no longer see any part of the superstructure of the bathyscaph through my porthole, but Piccard, who was in a much better position

to see the white-painted afterballast tank about 3 m away through his porthole, reported that he could still perceive its outline dimly. However, even this faded at a depth of 525 meters, so at this level we entered the zone of complete darkness for our non-dark-adapted eyes. On a subsequent dive nearby, A. Rechnitzer found that the threshold of his "seeing" was not passed until a depth of 600 meters. Similarly, Piccard found 600 meters to be the lower limit of his ability to detect any ambient daylight on one of his 1956 dives. William Beebe (1935) in his deepest dive to a depth of 3,025 feet in the Sargasso Sea off Bermuda, reported complete darkness at a depth of about 1,950 feet or a little less than 600 meters. He reported that at 1,900 feet there was still the faintest hint of dead gray light which was 200 feet deeper than he had usually recorded the penetration of light, but at 2,000 feet there was complete blackness. Feeding habits of shallow water fish in aquaria has suggested that their vision has about the same sensitivity as the human eye, but recent work by Denton and Warren (1957) at Plymouth, England, have suggested that deep-sea fish have eyes which are considerably more sensitive. By studying the photosensitive eye pigments, they have concluded that the eyes of deep sea fish may be sixty to one-hundred-twenty times as sensitive as the human eye and that such fish may be able to perceive daylight at a depth of about 1100 meters.

Between the depths of 500 and 700 meters the bathyscaph definitely appeared to be passing through a rich zooplankton zone. As the descent continued, scattering particles became noticeably sparser between 700 meters and the bottom. It should be emphasized, however, that because the scatterers are made apparent by the Tyndall effect, it may be impossible to make a valid comparison between the near-surface zones which receive some sunlight and the completely dark great depths. For example, one is completely unaware of the dust motes in a room unless it is darkened and a beam of light permitted to enter; the presence of any ambient light in the room would spoil the Tyndall scattering effect. Similarly the best "seeing" in the ocean obtains under conditions of complete darkness. However, the discovery of this rich zooplankton zone immediately below the ocean twilight realm is in accord with observations made from the French bathyscaph F.N.R.S.-3, such as for example, those of Bernard (1955).

The presence of this rich zooplankton zone is probably significant in connection with the oceanic phenomena termed the "deep scattering layer" or DSL. The DSL is an almost constantly present diffuse acoustic scattering layer lying between 150 and 300 fathoms in the open ocean. It is known to be caused by biological scatterers since it is most intensively developed during the day and, in large part, it migrates to the surface at night. Like many problems, the mystery of the DSL has in some respects become more obscure and is still far from final solution, but it is evident that it is a complex biological population in which at least euphausiids and certain deep-sea fish such as the myctophids are important. Apparently much zooplankton seeks the protection of darkness provided by deep waters during the day and rises to the surface at night to forage in the diatom-rich surface layers. Thus, it would be most instructive to make some bathyscaph dives at night to study the changes in this zooplankton-rich zone. Also comparable observations could then be made all the way from the surface to the bottom without the interfering effect of ambient sunlight.

While passing through this zooplankton-rich zone, the writer did not see any organisms of sufficiently large size to be good potential sound scatterers. Since, for a particular wave length, the scattering of sound varies as the inverse fourth power of the size of the target, an organism of suitable size to be a good scatterer for a 15 kc echo sounder should be at least 2–3 cm long, but no zooplankton of that size was observed. It is perhaps not surprising to see so little evidence of the DSL than the zooplankton-rich zone that was observed. Because of the lack of surface run-off, temperature instability, tides, and other factors which tend to cause upwelling, the Mediterranean has a notably low total organic production. For example, it is only about $\frac{1}{8}$ as productive as the Atlantic Ocean off Spain.

At D + 55 minutes we reached a depth of 900 meters. Here the echo sounder was switched on and we could see the bottom echo recording on the 100 fathom scale. The echo sounder has a maximum depth range of 100 fathoms, or 180 meters, so that it would have been useless to turn it on any sooner. We were descending rather fast. To slow us down for this bottom approach, Piccard jettisoned several kilograms of iron shot. A little too much ballast was dropped at one point so that the TRIESTE's descent was entirely arrested and we then began to rise slowly. This made it necessary to valve off some gasoline from the central tank to decrease our buoyancy.

Forty meters above the bottom a small fish came into view. Deep-sea fish are noted for their grotesqueness, but this one had a normal and attractive appearance: it was black and mottled near the head and colorless and translucent in the rear half of its body. It was a small fish, probably about two inches long, but as Hjort emphasized many years ago deep-sea fish are in general a "Lilliputian" fauna. I should note, however, that it is difficult to get a precise impression of the size of any organism through the porthole because one cannot easily judge the range, and there is nothing in the field of view to provide a comparative scale. Also one must add ⅓ for the foreshortening effect owing to the 1.33 index of refraction of sea water. The size stated here is based on the belief that it was about two feet away. By later examining Dr. N. B. Marshall's collection at the British Museum the fish seen appears to be a gonostomatid, close to the genus *Bonapartia*. This genus has not been previously reported from the Mediterranean but is common in the Atlantic outside of Gibraltar.

By D + 72 minutes we were 10 meters above the bottom and too close for the echo sounder to resolve it from echo returning from the TRIESTE's understructure. The "touch down" was made a few minutes later at D + 75, at 1100 meters. Piccard accomplished the landing entirely "on instruments" and it was so gentle that no jar was felt. The writer was unable to sense visually by staring through the porthole if we were descending, rising, or hovering, as there were few scattering particles to provide reference points for determining our motion. The sea floor appeared when we were only about three meters above it. It came into view slowly, at first fuzzy and indistinct and then sharp and well lit—like a photographic slide coming into focus. The bottom was quite smooth and muddy and appeared to be buff in color. (The coloration was later confirmed by a sample of buff silty clay with a few foraminifera "shells" recovered from the guide rope.) The sea bed was covered with numerous hummocks, probably six inches high and as large as two feet across. Some of them had central holes and were obviously built and presently occupied by some sub-bottom dwelling animal. The sea bed was completely barren of any visible life except for two white objects about the size and shape of butterfly cocoons. They definitely were not any type of mollusk and they could scarcely be siliceous sponges as these are rock-loving. Probably they were some type of mud-eating heart urchin.

We slowly settled into the bottom. A mud cloud was stirred up which quickly rose to the level of the porthole and obscured further vision. The depth of sinking of the TRIESTE into the bottom was only a few inches. Within a few minutes Piccard had adjusted the TRIESTE's buoyancy so that we were resting on the guide chain about three meters above the bottom. This was a remarkable demonstration of buoyancy control because the 20-meter-long guide rope weighs only about one kilogram per meter. In contrast the bathyscaph has a total mass of about 50 tons. The electric propellers were then turned on for a couple of minutes in order to move away from the enveloping mud cloud into clear water.

At this time the writer caught a fleeting glimpse of a fish about one foot long. Since it was on the bottom, one could get a good concept of range and scale. By sinuously thrashing about it stirred up the bed apparently to feed on buried organisms in the substrate. The fish was black and had a bull head like a catfish, but no barbels or tentacles were apparent. From a large head it tapered into a thin fleshy tail, but it

was definitely not of the rat-tail type. It seemed to me that it was some type of bottom-dwelling deep-sea angler fish. It was completely oblivious to the presence of the TRIESTE and to the floodlights. Subsequently, I also discussed this fish with Marshall who agreed that it was most likely some type of pediculate angler fish. The term "she" could probably be used advisedly, for Ragen (1925, 1930) long ago discovered that in at least four families of angler fish the male is a small parasitic form permanently fused to the female.

Several minutes later a little ballast was dropped to raise the craft a few meters higher on the guide rope and to offset the settling due to cooling of the gasoline, but because we rose to a height of about 20 m it was necessary to valve off a little more gasoline to sink to the bottom. During this maneuver I noted that there definitely was no crystal-clear layer of bottom water here as often has been reported by French bathyscaph observers on the F.N.R.S.-3 (Peres and Piccard 1956). They have frequently reported a bed of water several meters thick lying in contact with the bottom which appears to be crystal clear, *i.e.*, completely without any scattering particles and in contrast to the more turbid water above. This crystal-clear layer is a remarkable discovery for which there still is no satisfactory explanation. However, as the French divers are well aware, this observation must be carefully made since the observer might become so intensely preoccupied with staring at the bottom that he is no longer consciously aware of any scattering particles in the water.

Once again on the bottom, a third small fish appeared in view at close range. This one was the same type as the first fish, that is, probably a gonostomatid close to the genus *Bonapartia*. Also, a small one-inch-long shrimp swam past in a zigzag fashion about a foot above the bottom. When the lights were extinguished an occasional bioluminescent flash could be seen, but these were rare. No noise could be heard except for the slight and reassuring hiss of the escape of oxygen from the battery of oxygen bottles. We were perfectly stable and below any threshold of accelerations that I could detect by the "seat of my pants"; but the stability nonetheless is probably not good enough for many precise geophysical observations.

At 1706, after having been on the sea bed for 36 minutes, we dropped ballast and began the ascent to the surface. The time on the bottom was shorter than desirable, but we had to return to the surface before nightfall in time to prepare the bathyscaph for the long tow back into port. When the ballast struck the bottom about 20 small animals, looking like grains of rice, and which had not previously been visible swam off the bottom in a steady but random fashion above the mud cloud that was forming. I assumed that these small animals probably were either amphipods or isopods that live in the substrate. Most likely they were isopods for Rechnitzer observed swarms of them on subsequent dives.

As the TRIESTE rose off the bottom, a boiling turbid mass of mud formed. The shape was that of an expanding and turbulent doughnut spreading from the point where the ballast had fallen. It was a visual demonstration of a small force setting up a dense cloud of mud which might easily have been transformed into a turbidity current on a sloping bottom. But as we quickly rose the mud cloud faded from view.

Looking out the window, it seemed that at times we were rising, then hovering, then descending again. This was at first quite alarming, but the instruments showed a uniform continuous ascent. It then became evident that the TRIESTE entrains a burble or knuckle of water in her wake as she rises, which makes it impossible to judge visually from watching the scattering particles in the water whether the craft is rising or settling. Because of this turbulent eddy the ascent is a poor time to attempt to make precise observations. However, it did seem feasible to get an over-all impression of the density of life at different levels. One manner of obtaining some quantitative concept of the number of small scatterers in the water was to turn on the far floodlight in order to gain an impression of the strength of the Tyndall scattering. The light cone was found to be equally bright at all levels until ambient sunlight interfered with the

observation. This may be largely explained as scattering from molecules of dissolved high polymers or macromolecules and from colloidal particles.

Porthole observations were also being confused during the ascent by pieces of mud which were constantly being washed off the craft and which would stay in the view for many seconds entrapped in the turbulent wake of the TRIESTE. An advantage of this eddy is that it stimulates many light-producing organisms to display their luminescence. When the floodlights were off blue-white flashes could be seen every several seconds. Watching the frequency of these, it seemed that the amount of bioluminescent life in the water increased as we rose and reached a maximum between 700 and 500 meters—or at the same level where the maximum of life had been noted during the descent.

At a depth of 450 meters Piccard first reported seeing the outline of the ballast tank, and by the time 300 meters was reached there was sufficient ambient daylight so that the outline of the understructure of the craft was plainly visible. As we rose our speed of ascent continued to accelerate since the petrol was expanding and increasing our buoyancy. The only organism noted near the surface was a medusa that floated by at a depth of 64 meters.

At 1746, that is, 40 min after we left the bottom and 2 hrs 31 min after the dive began, the TRIESTE hit the surface; its arrival was marked by a gentle deceleration. We had passed through the thermocline a few moments before, although there was no visual evidence of it. Piccard then blew the air lock clear of water with the compressed air bottles so that we were able to open the cabin door and climb up to the deck of the TRIESTE to await the arrival of the Italian Naval tug, TENACE, the escorting vessel.

Perhaps it is worthwhile to record a few over-all impressions of the dive. It was entirely comfortable and unadventurous, and the cabin was amply roomy so that there was never any feeling of claustrophobia. I believe that a person could be quite content in it for at least 24 hours and perhaps longer. I must confess to occasional awareness, and hence mental anguish, of the tens of thousands of tons of hydrostatic pressure squeezing the cabin. However, it is a source of great assurance to have a detailed knowledge of the excellent design and construction of the TRIESTE where 99% certainty has not been considered to be good enough. Professor Auguste Piccard, Jacques' father, deserves great credit for solving the problems posed by the tremendous pressures of the deep sea and for constructing this vehicle safe enough to permit manned descent.

Difficulties with the bathyscaph are almost invariably connected with its surface operation and it is apparent that this craft will not fully come into its own until it can break away from the requirements of operating with a surface ship. For example, three days out of four are lost simply waiting for suitably quiet surface conditions of wind, wave, and swell.

A basic restriction on the maneuverability of the TRIESTE was imposed by the large size of the gasolene-filled float. It would seem to me that future deep-sea research craft should try to dispense with such cumbersome floats and carry only enough gasolene for buoyancy control. Such a craft could be built on the principle of one or more buoyant spheres in series and be designed to operate on or along the bottom. Present technology of metals might now restrict such the craft from the great depths, but future improvements in metals should make these accessible. Since such a craft differs in basic principle from the bathyscaph it could reasonably be termed a *bathynaut*.

One important result of my dive was the realization that the ocean can be divided into three life zones based on the penetration of daylight. The uppermost of these is from 0–200 meters and can be termed the *phytophotic* zone. This corresponds to the euphotic zone and is the layer in which daylight is strong enough to permit photosynthesis. This zone forms the pasturage of the sea, and all marine life is ultimately dependent upon it. The second zone extends from 200 meters down to about 900 meters in the clearest water but much less in turbid water. It can be termed the *zoophotic* zone. Here animals are generally aware of the day-night

astronomical rhythm, and a part of the population undertakes daily migrations to the surface. The concentration of scattering particles that I noted on my dive and which the French have also reported from dives in the FNRS-3 marks the bottom of the zoophotic zone. Many animals apparently utilize the cover of almost complete darkness for security; and the larger ones form the scattering cloud known as the deep scattering layer. Finally extending from 900 meters to the bottom, there is what might be termed the *aphotic* zone which is the region of complete darkness. Here animals can have no awareness of the day-night rhythm and the "clock mechanism" so widespread in nature must be absent. One would suspect that this is the realm of the truly abyssal-pelagic animals and that they differ considerably from those which inhabit the zoophotic zone. There would seem to be little reason for them to perform purposeful migrations, and certainly such migrations as do take place cannot be rhythmically controlled by daylight.

Dismissing the pressure factor, one cannot help but be impressed by the friendliness of the deep sea environment. It is quiet, calm, and serene. The deep sea also is timeless in the sense that the activity of life outside the abyss is controlled by astronomical time rhythms of the day and of the year, which have no meaning in the deep sea. It was this rhythm, the coming of night, which made us break off our dive sooner than we would have liked and "fall up" to the surface.

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Natural Water as a Monochromator[1]

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ABSTRACT

Many of the spectral data on the optical constants of natural water are suspect because of errors introduced by light "leakage" outside the stated band of the filter used. The magnitude of this error is computed for a specified water sample under specified natural lighting when measured with a specified detector and filter. The errors are large even for measurements at shallow depths. Methods for avoiding this error are suggested.

For the past twenty years, at least, there has been considerable interest among biologists and oceanographers in measurements of the spectral distribution of natural light in lake or ocean water. It has been common practice in making such measurements to employ glass or gelatine filters over a photo-detector for the purpose of isolating certain spectral regions. More recently interference filters have been substituted to take advantage of the narrower band widths offered by these filters and also to minimize the confusion in assigning a wavelength to the experimental data.

All too few workers have been aware of the pitfalls of this procedure. Some, it is true, realize that their wavelength assignments are not "quite" correct because of "band-width error," as it has been called, but the devastating effect of "band-width error," or "leakage," or "stray light," or whatever one chooses to call it, on deep water data just has not been made obvious.

The purpose of this paper is to demonstrate the magnitude of band-width error on deep water data and to suggest ways of avoiding it.

Two basic thoughts should be evident in what follows:

(1) The experimental values obtained by a photodetector lowered into water will be directly proportional to the summation of the wavelength-by-wavelength product of four wavelength-dependent parameters, *viz*:

(a) the spectral energy distribution of the natural light that gets through the air-water interface (E_λ),

(b) the spectral sensitivity of the photodetector (S_λ),

(c) the spectral transmittance of the filter employed for band-width isolation (T_F), and

(d) the spectral transmittance of the layer of water between the instrument and the surface (T_W).

Thus any experimental value V can be expressed as follows:

$$V = C \sum_{\lambda_1}^{\lambda_2} E_\lambda S_\lambda T_F T_W \, \Delta\lambda \qquad (1)$$

where C is a proportionality constant, and the limits λ_1 and λ_2 are established by one or more of the four parameters.

(2) Deep water is sometimes far better as a monochromatic filter than a glass or gelatin filter, and although the purpose of the filter (T_F) is to control the spectral band width, actual control may in fact be imposed by the water itself.

Let us go back for a moment to the first of these thoughts. It should be obvious that every light measurement (V) will be associated with some spectral distribution. That is to say, as you proceed from one end of the spectrum at some wavelength (λ_1), the value of the product of the four parameters listed above will become a significant part in the measured value V. In the usual case the product will then remain significant throughout some band of wavelengths, but will finally drop until at λ_2 the product has no more significance than it had at λ_1. The measured value V must therefore be associated with the wavelength band

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between λ_1 and λ_2. Also, since the curve of the product vs. wavelength changes with depth, the light measurement will be associated with a different band width at each depth.

If values of the independent parameters are available over a wide spectral range, one can determine the spectral band to be associated with V by computing and plotting this product, $E \cdot S \cdot T_F \cdot T_W$. If this is done at selected depths, the change in the band width and its position in the spectrum can be observed.

The parameters have been defined in such a way that the only one that varies with depth is the transmittance of the water layer between the instrument and the surface (T_W). This transmittance is ordinarily measured with a horizontal cosine collector (flat-plate collector), and the equation used to express the relationship between transmittance and depth is the familiar exponential law

$$T = e^{-kz} \qquad (2)$$

At the present time there is not available a complete table of spectral data for the coefficient k or for the transmittance expressed above. In order to demonstrate the importance of band width error it will be necessary to use some reasonable approximation to such data. Measurements on various bodies of natural water made by this laboratory indicate that at a wavelength of approximately 500 mμ the value of k is about one-half the value of the beam transmission coefficient, α. For the purposes of this calculation the beam transmission values given by Hulburt (1945) have been multiplied by one-half to obtain a table of k values as a function of wavelength. The shortcomings of this approximation will probably be obvious enough. For example, the procedure does not take into account the selective scattering of blue light which would tend to decrease the values of k in the blue region relative to the red region of the spectrum. However, although a factor of 2 in the value of k could alter the present example in detail it will not invalidate the result.

This approximation for spectral values of k has been used together with: (a) spectral

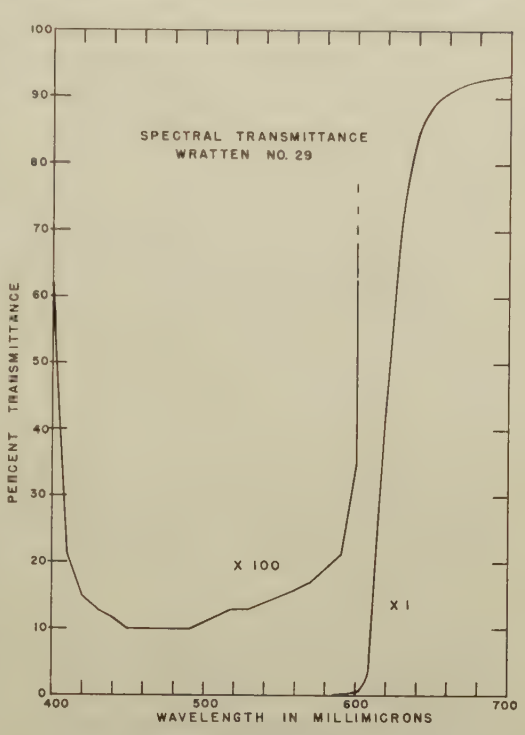

FIG. 1. Spectral transmittance curve for a Wratten #29 filter. The table of published transmittance data for this filter shows no values between 400 and 600 mμ.

data on the energy distribution of natural illumination taken from the *Handbook of Colorimetry* (Hardy 1936); (b) spectral sensitivity data for an RCA 931A multiplier phototube, from the book *Photoelectricity and its Application* (Zworykin and Ramberg 1949); (c) spectral data for a typical "sharp cut-off" red filter (Wratten #29) shown in Figure 1. Using these data the product $E \cdot S \cdot T_F \cdot T_W$ has been computed at 10 mμ intervals. The results of this calculation, after normalization to 100%, are plotted in Figure 2. The effect of the transmittance of three meters of water is almost completely lost compared to the major effects introduced by the multiplier phototube which cuts off the far red end of the spectrum and the Wratten #29 filter which cuts off the blue and green. However, it should not be overlooked that 18% of the signal is coming from wavelengths between 400 and 600 mμ. It should be remembered that the purpose of making these measurements is to determine the transmittance of the water to light

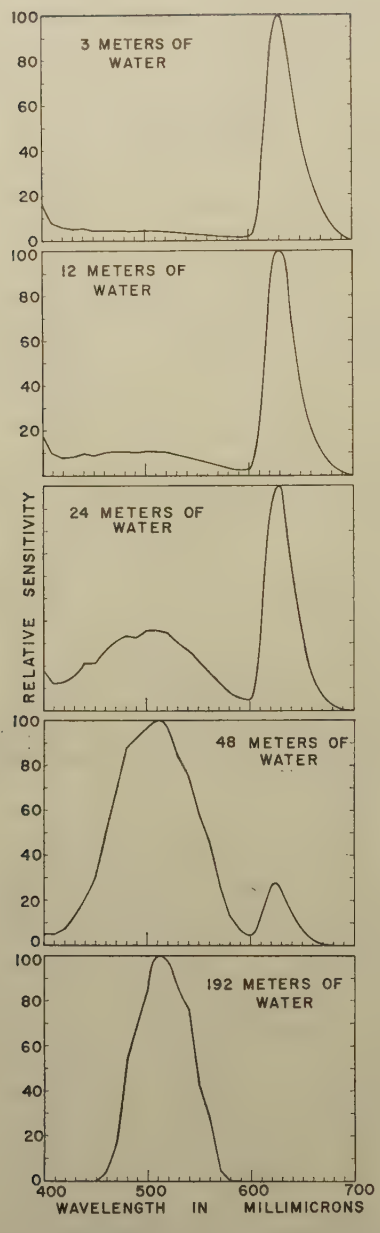

FIG. 2. Relative spectral sensitivity characteristics of a photoelectric detector unit consisting of a multiplier phototube with spectral sensitivity S_{931} equipped with a Wratten No. 29 red filter having transmittance T_{29} when used at five different depths. The spectral distribution of the surface light is defined as E_0 and is fixed. In each case the signal obtained is proportional to the area under the curve and is consequently tagged with the spectral distribution indicated by the limits of the curve.

of a selected band width which has been experimentally specified by the combined spectral characteristics of the filter and the photo detector. If there is a significant relative amount of light leakage outside this selected band an error will be introduced into the reading. In the present example the measurements would normally be assigned a wavelength band between 600 mμ and 700 mμ. Hence the signal coming from wavelengths between 400 mμ and 600 mμ represents an 18% error in the measurements taken with this filter-phototube combination in three meters of ocean water. In twelve meters of water the error has risen to around 32% with the peak wavelength of the major band remaining nearly constant. At a depth of 24 meters the error is around 56% which means that there is more energy being measured outside the red band than is being measured within the band. At 48 meters the measurements have nothing to do with red light at all and at 192 meters we discover that we are measuring monochromatic light of wavelength 510 mμ and half band width of 70 mμ, which is better monochromatic light than was initially provided by the combination of the transmittance properties of the filter and the response properties of the photocell. The interesting result that derives from this example is that no matter what filter or what detector one starts with, if measurements are made deeper and deeper in this water one can look forward to measuring monochromatic light of wavelength 510 mμ at some predictable depth. It follows that for deep-water measurements one must design the optical filter with as much care as was used in designing the mechanical components to withstand the pressure. Otherwise the optical filters will "fail" just as surely as a weak mechanical structure would fail when used at too great a depth.

The effect of this error can be detected in the experimental data of many contributors to the literature on measurement of light in the sea. One example will serve to illustrate. Using the ocean described spectrally above, suppose one measures the upwelling light from the sea and the downwelling light

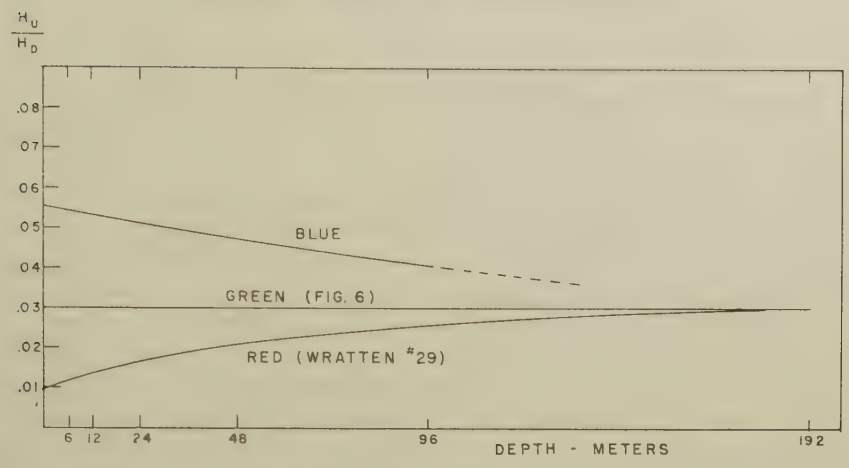

FIG. 3. An example showing the effect of "band-width" error on deep water data. The ratio of upwelling irradiance (H_u) to downwelling irradiance (H_d) is commonly thought of as the reflectance of the water at a horizontal plane beneath the surface. In homogeneous water this reflectance would be expected to remain constant at any one wavelength. In this example as the band width shifts from red to green the ratio H_u/H_d increases accordingly.

from the natural field above in an effort to determine the ratio of these two quantities as a function of depth in homogeneous water. Suppose this work is done using three filters: the Wratten #29 red filter described above, a blue filter having normal leakage characteristics, and a green filter whose transmittance happens to be identical in form with the curve for 192 meters in Figure 2. Near the surface, measurements with these filters will show that the ratio of the upwelling irradiance to the downwelling irradiance (H_uH_d) in the blue region is high (due to the high degree of blue scattering), that the ratio is smaller when the green filter is used, and much smaller with the red filter. Due to band width error, measurements with the red filter at a depth of 192 meters will be tagged with the same spectral band as measurements taken through the green filter, and the two ratios will therefore be the same at 192 meters. Ratios obtained through the blue filter will, for the same reason, exhibit a trend toward the green ratio as depth increases, but may not have reached this ratio at 192 meters, depending on the specific properties of the blue filter. A plot of H_u/H_d vs. depth for the three filters will therefore look like Figure 3.

The design of optical filters for deep water use requires a detailed knowledge of the transmittance properties of the optical components. The transmittance of the filter should be known even though it is only 0.01%. With this information a filter can be designed by combining several separate filters having desirable characteristics. The combination can be made to have minimum transmittance except in the spectral region under study. With such filters one can have confidence in the near-surface values of k (for example). These values can then be used to estimate the band-width error at greater depths, and also the depth beyond which the filter should not be used.

If data within a narrow band are wanted, but the position of the wavelength band is not important, a filter can be used which duplicates the pass band expected for deep water. Such a filter will make the data consistent in band width at all depths.

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National Science Foundation Travel Grant

The XIV International Congress of Limnology will be held in Vienna, Austria, August 21 to September 2, 1959. The American Society of Limnology and Oceanography, Inc., has received a grant from the National Science Foundation to defray cost of coach-class air transportation for about twenty persons. A committee of five, appointed by the President of ASLO, will receive and evaluate applications for these travel funds.

General considerations guiding the selection of applicants will include: (1) Interest and activity in limnological research or applied limnology, (2) Need for financial assistance in making the trip (those who can get this transportation paid otherwise should not apply), (3) Receipt of applications by March 16, 1959.

Those selected will include younger scientists of promise as well as individuals with a longer history of research. Members and non-members of ASLO, residing in the United States and Canada, are eligible.

Application forms and additional information about these funds may be obtained by writing the Secretary of ASLO.

Communication concerning a Central Agency for C^{14} determination (Measurements of primary production in the sea) at Charlottenlund Slot, Denmark

During recent years the study of the primary production in the sea has been one of the main concerns of marine science. The present great interest in productivity is due *inter alia* to the use of the radioactive tracer C^{14} as a tool for measuring primary production in the sea regardless of the size of the production. Steemann Nielsen first employed the C^{14}-method for measuring the production of organic matter in the sea on the deep-sea expedition of the "Galathea" 1950–52. The technique has now been used by many investigators all over the world, and it has been routinely included in oceanographic data-gathering voyages and on light ships, where the field work is made by the crew.

The most recent description of the different modifications of the C^{14}-method is found in the articles B.2 and B.3 in "Contributions to Plankton Symposium 1957, Measurements of Primary Production in the Sea." Rapp. et Procès-Verbaux des Réunions (Cons. Perm. Intern. p. l'Explor. de la Mer), Vol. 144, 1958.

An important factor in the usefulness of the C^{14}-technique for measuring primary production is that the field work does not presuppose any expert knowledge. On the other hand, the manufacturing of the ampoules containing the solution of $NaHC^{14}O_3$ to be used for experiments requires a well equipped laboratory and a scientist familiar with radioactive tracer work. The same is true concerning the measurements of the radioactivity of the filters containing the samples.

Whereas large oceanographic institutions ordinarily will have such an expert at their disposal, this will not be true for many other marine laboratories. In several instances therefore various institutions have cooperated. The ampoules to be used have been manufactured at one place and sent to another where they have been used for productivity work. The dried filters with the radioactive plankton have in turn been sent back to the first place for measurement. As the half-life of C^{14} is more than 5000 years, the filters, if properly stored, remain unaltered for a very long time.

During the symposium on "Measurements of Primary Production in the Sea" held at Bergen 27–29 September 1957 by the International Council for the Exploration of the Sea, an *ad hoc* working com-

mittee was appointed to deal with the methods for the measurement of primary production. The members were: John H. Ryther (chairman), Grim Berge, Maxwell S. Doty, G. E. Fogg, and E. Steemann Nielsen.

The committee presented recommendations which were adopted unanimously by the approximately 80 participants of the symposium. One of the paragraphs read: "It is suggested that a central agency be established, for example at Charlottenlund under the direction of Prof. E. Steemann Nielsen, which would provide standardized ampoules of C^{14}, counting of C^{14} samples, and calculation of carbon assimilation rates."

In January 1958 UNESCO provided funds for establishing the Agency. The "Danish Institute for Fisheries and Marine Research" provided a room at its residence at Charlottenlund Castle, Denmark.

The Agency is organized on a non-profit basis. Professor E. Steemann Nielsen, who is adviser on plankton research to the "Danish Institute for Fisheries and Marine Research," will be honorary supervisor. The daily work will be directed by Mr. Vagn Hansen of the same institute. The facilities of the Agency, which will be officially opened during the meeting in October 1958 of I.C.E.S. (The International Council for the Exploration of the Sea), are available to all scientific institutions in the world. The consignments will be made in accordance with rules set up by the Danish Ministry of Health.

Standardized ampoules of C^{14}—activity 0.004 mc.—may be obtained from the Agency at the following prices:

100 ampoules or more	D.Kr.	2.75 each
50–99 ampoules	D.Kr.	3.00 each
less than 50 ampoules	D.Kr.	3.25 each

If the purchaser wishes to have the filters containing the samples from experiments counted by the Agency the total price (including ampoules and numbered membrane filters) will be:

100 ampoules or more	D.Kr.	5.00 each
50–99 ampoules	D.Kr.	5.25 each
less than 50 ampoules	D.Kr.	5.50 each

The prices include packing but exclude transport. Special boxes for the return of the filters when the counting is to be done by the Central Agency will be provided.

The salinity of the sea water used for the experiments must be stated by a customer. It will be sufficient for water from the open ocean to designate "ocean water." The photosynthetic rate will be computed by the Agency. When using either brackish water or fresh water it will be necessary for the customer to determine the total concentration of carbon dioxide in the water.

The water samples to be used for the experiments should be taken with a glass, plastic, or other type non-metallic, non-toxic sampler.

Directions for use of C^{14} tracer will be enclosed in each consignment.

A filtration apparatus operating by pressure obtained by a bicycle pump may be provided from the Central Agency at a price of D. Kr. 300.00.

Special holders to be used when drying filters may be obtained at a price of D. Kr. 8.00 each.

A suitable water sampler may be provided by Laboratoire Hydrographique, Copenhagen, at a price of 830.00 D. Kr.

Field kits for sample collecting, filtration apparatus, filters, etc. may also be provided, on request and at cost price, by Prof. Maxwell S. Doty, Botany Department, University of Hawaii, and by Dr. John H. Ryther, Woods Hole Oceanographic Institution, Woods Hole, Mass. U. S. A.

HUTCHINSON, G E. 1957. **A treatise on limnology. Volume 1. Geography, physics and chemistry.** 1015 pp. Wiley, New York. $19.50. Chapman & Hall, London. 148/–.

The development of the twin sciences which make up the title of this journal owes a great deal to monographic works which aimed to provide, for their time, a comprehensive account of the physics, geology, chemistry, and biology of a lake microcosm or of the ocean macrocosm. Forel's "Le Léman" and Murray & Hjort's "The Depths of the Oceans" are notable early examples, while Sverdrup, Fleming, and Johnson's "The Oceans" is the best known contemporary one. These works created eminences from which the topography of the whole subject could be viewed. Professor Hutchinson's two-volume "Treatise on Limnology" will, when complete, enter this distinguished category. His aim is "to give as complete an account as possible of the events characteristically occurring in lakes"—no less. This is a formidable task for one author, but those who know Hutchinson's researches and writings on limnology and cognate fields of ecology, lake history, and biogeochemistry will anticipate a comprehensive, scholarly, and integrated account. In this first volume they will not be disappointed. This treatise is the fruit of many years of research and literary labour, and it has proved necessary to publish it in two volumes. The volume here reviewed covers geographical and physicochemical limnology. The second volume, yet to appear, "will deal with limnobiology and the ecological, typological, and stratigraphic problems of lake development." The whole work is addressed, not to limnologists alone, "but also to biologists who may wish to know something of the physicochemical environment, mode of life, and evolutionary significance of such fresh-water organisms as they may study from quite different points of view; to geologists who are desirous of learning something of modern lakes in order that they may better interpret the record of inland waters in past times; and to oceanographers who wish to compare the results of their own science with what has been learned of the small but very individual bodies of water which make up the non-marine part of the hydrosphere."

Written as a comprehensive treatise on physicochemical limnology for the advanced student, the text carries much detailed exposition aiming to provide a background for research; but concise, factual summaries are presented at the end of each chapter. These should prove helpful, not only to the general reader or the elementary student, but also to many who will use the volume for reference, for they will find the index to be inadequate for a work of this size and detail. The bibliography covers a wider field than any hitherto published, and is as fully international as the author could make it—a welcome change after the insularity of some earlier European and American texts—although post-war Russian literature remains regrettably largely unavailable, and few papers published after 1955 could be considered. Lists of symbols used and of organisms and lakes mentioned in the text complete the indices.

But this book is much more than a comprehensive work of reference. The author's selection and masterly integration of material from many realms of knowledge lends it a personal quality in which *cognoscenti* will recognize many familiar features of Hutchinsonian style: a flair for concise presentation of essential findings in complex or remote fields of research; a proper regard for pioneers (*e.g.* pp. 299, 426); a love of curiosities (*e.g.* "lake guns" p. 361, *fata morgana* p. 420); a wide use of mathematical formulation and models; a predilection for the adoption or invention of special terminology, which here usually clarifies and rarely confuses. The personal quality of this synoptic view would have been lost in a symposium volume.

In some respects the necessity to publish the work in two volumes is regrettable, for it would have been more satisfactory to consider many of the chemical processes alongside the organisms engaged in them. However, the author promises to "revert to certain chemical matters" in the second volume and to take that opportunity of bringing the first volume up to date. In spite of their high price, the two volumes will certainly form an important part of limnologists' equipment and will continue to stimulate research and teaching, not in limnology alone, for many years to come.

The remainder of this review is taken up with comment on range, emphasis, and detail, with most of the space devoted to the reviewer's special interests in the physical chapters. Other sections are correspondingly neglected. A balanced critique of the whole volume would require the combined efforts of several specialists—physical geographers, hydrodynamicists, geochemists—, and the reviewer has been fortunate in having some comments from Dr. J. Talling and Mr. F. J. H. Mackereth on the optical and chemical chapters, respectively. Page numbers are shown in parentheses; references not included in the author's bibliography are listed at the end.

Apart from a short chapter on the structure, properties, and isotopic composition of natural water, the first quarter of the volume is entirely devoted to the physical geography of lake basins: origins and mechanics of formation; morphometry and morphology; water balance and the hydrological cycle. In all, seventy-six types of basin are systematically described "according to the general nature of the processes responsible for building, excavation and damming. Since these processes have acted locally, the resulting classification tends to be regional." Excavation and damming by ice action during the Pleistocene glaciations were responsible for the formation of

far more basins than all the other agencies together. Morphology was determined partly by the forces which created the basin and partly by forces associated with wave action and inflowing streams which commenced operation as soon as the basin was formed. These forces are far from thoroughly understood, and the author does not attempt to review more than a small selection of the extensive literature. The importance of catastrophies could have been emphasized more. Great storms or floods can have more effect on morphology than many years of ordinary weather, and the sudden bursting of morainic or outwash dams may be the true explanation of the origin of some of the large "deltas," now associated with small inflows, in some glacial lakes (185). "Ice push," an important shore-moulding force in some lakes today, and in many more in immediate postglacial times, could have been included by cross reference (532).

The second quarter of the volume, which forms the backbone of the work in the sense that the events described in later pages must fit into this physical framework, comprises three closely linked chapters on the hydrochemical, optical, and thermal properties of lakes. Discussion of optical properties commences with the spectral distribution, the intensity, and the fate of solar radiation arriving at the lake surface. The discussion proceeds in logical sequence, by way of laboratory studies of selective absorption in pure water and natural lake waters, to the main theme —the underwater light field and the factors which determine it. This clear and factual account raises few conflicting interpretations, but some of the space devoted to laboratory measurements (381–8) could have been better used to expand the all too brief discussion (392–6) of the distribution, and particularly the spectral composition, of subsurface illumination in nature. This is the key to the understanding of lake (or marine) optics, and it forms a logical starting point for a comparative study of optical diversity in lakes. For example, the complex concept of "white light" extinction (392–5), and the criteria to be applied to measurements with receivers of restricted spectral sensitivity, would have emerged more clearly if they had been derived from the data of spectral extinction, rather than the other way about.

Also, the detailed mathematical treatment of scattering (404–6), which the original author relegated to an appendix, could profitably have made way for a discussion of experimental work on scattering (Atkins & Poole 1952, 1954; Jerlov 1953) and its effect on the angular distribution of underwater illumination (Whitney 1941) and on the differences between laboratory extinction coefficients and those determined in nature.

Other investigations—mainly marine but immediately relevant to the author's theme—include: Clarke and James (1939), probably the most reliable determination of the spectral absorption of pure water, which yields an extinction coefficient in the blue region of about twice the value inferred at the bottom on p. 393; Le Grand (1939) and Moore (1947), the relation between extinction, turbidity and Secchi disc readings; Clarke (1939), a review with valuable unpublished data from James and Birge.

Speculation, largely absent from the chapter on optics, is more evident in the chapters on hydromechanics and thermal properties. These are the two longest chapters, together comprising 231 pp. The first is concerned mainly with the laws of fluid motion as influenced by gravity, wind stress, and the earth's rotation; while the second deals mainly with observations of stratification, heat exchange, and freezing. Material for these chapters has been assembled from widely scattered studies in physics, hydrodynamics, meteorology, limnology and, notably, oceanography. Although many of the key processes are imperfectly understood, and although this leaves much scope for debate and more for research, the reader will not find elsewhere a more comprehensive account of the physical framework within which the chemical and biological events in lakes must run their course. It would be a pity, therefore, if he were to shy at the author's frequent use of the language of mathematics. The treatment is essentially nonmathematical, and the conclusions are also expressed in words and diagrams.

The concepts of turbulence, the eddy spectrum, and the concomitant laws of non-Fickian diffusion are rightly placed at the outset (250–9), even though present knowledge of the eddy coefficients in lakes is meagre (466–78), and nothing is yet known about the distribution of turbulent energy within the eddy spectrum (259) or of the dependance of this on lake dimensions, stratification, and wind stress.

The short section on turbulence is followed by forty pages describing the three main types of current (gradient, wind, and density). The generous space (265–72) devoted to Ekman "spirals" —because of their theoretical and historical interest—should not lead the reader to expect to find them developed in textbook clarity in any real lake. The steady-state theoretical pattern will be greatly modified by shore constraint and by non-uniformity of vertical turbulence and wind stress. The author points out (270) that "most approaches to an Ekman current system that are likely to be observed, even in large lakes, are probably transitory phases in the development of a steady theoretical pattern," and he makes no attempt to relate the large-lake circulation patterns, illustrated on pp. 290–4, to the Ekman models. Incidentally, the thermocline configuration in Figure 81 B was probably the result of internal wave motion and not of the current system postulated on p. 294; a week later the section looked very different.

Research on the factors controlling the shear stress exerted by wind on the water surface actively continues, and additional observations are reviewed by Francis (1954), who elaborates the

view (352) that it is the small "roughness elements, the ripples," on the waves, and not the waves themselves (279), which are the main contributors to the drag (see also Charnock 1958). Van Dorn, whose paper (1953) merits more detailed consideration in a textbook of physical limnology, also found that driving rain appreciably increased the surface stress. The conclusions (285–6) on wind drift in a circular lake require further examination. If conditions are steady and if the wind stress is uniform over the whole lake, it is difficult to see why the tilt of the surface should not also be constant and exactly counter-balance the stress. In other words, the acceleration (equation 68) around the sides of the lake will be exactly balanced by the component of the wind stress in the opposite direction. However, if the wind field is assumed constant but its shearing stress on the water surface increases with fetch, a surface "return current" could run along the shore from the diametral region of longest fetch (and greatest stress) to the region of short fetch (and smaller stress). Further research is required to determine how shallow a basin must be to prevent the occurrence of subsurface return currents. A well developed subsurface current was observed in a model tank 44 cm deep (Francis 1953), and, in the absence of measurable bottom stress in his model-yacht pond (mean depth 185 cm), van Dorn (1953) concluded "tentatively that the bulk of the circulation . . . is confined to a relatively thin layer near the surface." A final comment on the current section is that it is potentially misleading to illustrate the circulation patterns in stratified basins (Figure 79 A and, particularly, B) if "there is considerable doubt about these observations" (282). Later remarks on the importance of the criteria of stability of flow in stratified fluids are relevant here.

The generous space allocated (299–311) to the surface seiche reflects the great interest which this phenomenon has had for limnologists and mathematicians since Forel first subjected it to scientific study. Much effort has been expended in devising methods of computing the free periods of oscillation in irregular basins. For instance, the considerable body of work (twenty-six papers, 1948–54) by Caloi and collaborators on surface seiches in Italian lakes, some of which are referred to in Caloi (1954), could have been mentioned. No doubt part of the attraction of this work lies in the ease with which the theories can be checked by observations, and this may explain why some investigators, like sorcerer's apprentices, have produced minor spates of papers in which the method has been applied to one lake basin after another without the emergence of any new principle. At least five distinct methods of calculating the free periods have been devised. The author bases his exposition on Chrystal's method alone, which although the first in the field is the least satisfactory, as it requires the basin geometry to be fitted to known curves. For practical purposes it would be better replaced by an iterative method, for example that used by Defant (1918), which can be applied to basins of any shape and in which the labour of computation can be adjusted to the degree of accuracy required. Caloi (1954) applies three of the methods to the same basin.

While the direct contribution of the surface seiche to the economy of lakes or to water movement in them is small (but see 329), its theoretical influence has been considerable. Somewhat paradoxically the main practical application of lake seiche theory has been in the investigation of tides. Its significance for the main stream of limnology lies mainly in the fact that the results and the methods can be applied *mutatis mutandis* to computations of the periods and amplitude distribution of internal seiches in actual basins. In contrast to the surface seiche, the internal seiche (this general designation is preferable to the alternative "temperature seiche" used in the book) plays a conspicuous part in movement and transport in stratified basins (337–41).

A word of caution is appropriate here. The uncritical use of the term "seiche" to describe any internal oscillation can be misleading. Both seiche types, surface (325–6) and internal, are most commonly set in motion by wind or by change of wind direction (for example, Darbyshire & Darbyshire 1957), and the response of the lake to the wind often takes a quasi-oscillatory form, depending on the timing and variations of wind force and direction. The picture is further complicated by the tendency of the layers to oscillate with their own free periods, *i.e.* to resonate, while the driving force is being applied. The resultant motion is made up of forced oscillations or displacements mixed with free oscillations, seiches proper, which persist and finally die away after the driving force has been removed. Without careful analysis of a long series of observations, it is often impossible to distinguish between the forced and free components, that is between wind effects and true internal seiches. This is particularly true of very shallow or complex basins in which the internal seiche is so heavily damped that only the "oscillations" forced by direct wind action are left, or in large basins where the seiche periods are of a similar time order to the intervals between wind storms. The examples quoted at the bottom of p. 339 and the later publication of Fish (1957) should be re-examined in the light of these remarks.

To interpret internal oscillations, a number of mathematical models have been devised. For many purposes the two-layered one (336–7) is adequate, but much closer approximations to nature are provided by the more generalized models of Fjeldstad (1933) and Groen (1948). These merit consideration at the expense of some of the space (341–46) devoted to the three-layered model.

Marine research on wind-generated surface waves received a great impetus from wartime

needs and instrumentation, and that impetus has continued into the post-war years. The author has, therefore, had at his disposal several good accounts which link theory and observation. While there are numerous studies on a model scale and a very large body of observations at sea, very few investigations have been made on lakes, possibly because suitable instruments were lacking. The author has selected limnological applications where possible, but apparently has not included publications later than 1952. Burling's (1954, 1955) investigation on a reservoir with an instrument recording frequencies up to 5 c/s, is therefore, of particular interest. His values for the age and height parameters lie considerably below Bretschneider's solid lines in Figures 106 and 107, but the curves are of the same form. (There is a trivial error in the vertical scale of Figure 106; the graduations should be labelled as in Figure 107). The most probable explanation is that Johnson (1950), on whose data Bretschneider's curve was based, used a pressure recorder which attenuated the higher frequencies, and made his measurements in unstable air (water considerably warmer than air). Under such conditions Burling found that, for a given wind speed and fetch, the wave period was slightly longer and the wave height considerably greater than under near-neutral or stable conditions. Burling's work is reviewed with other recent studies of wave statistics, generation and growth by Charnock (1958). This review, which contains much of relevance to lake conditions, is a most useful supplement to Hutchinson's account.

In the chapter on thermal properties limnologists will find themselves on more familiar ground. Here is unfolded in masterly fashion the classic picture of the lake seasons, of stratification, and of heat exchange. The thermal histories and representative temperature profiles of all types of lake are fully described. It is in their interpretation that the reader may find some confusion and difficulty. This is inevitable because, where the mechanics of flow and turbulent transport are concerned, "we now see through a glass darkly." Direct observations of motion in lakes are few (286–92), and where observations are lacking, debates grow long, for instance on such matters as the distribution of heat and solutes in the hypolimnion (478, 625, 675–7) or transport of these across the thermocline (466–75). This in itself is by no means uninstructive, but it is a sad comment on our present state of knowledge to find not more than two pages (255–6, 430) devoted to the concept of the Richardson number, which probably holds the key to the understanding of motion in stratified lakes.

Perhaps the best way to try and justify this comment is to point to the distribution of isotherms in a stratified lake, small enough for geostrophic effects to be neglected (Fig. 103, p. 344), or in a stratified model lake (Mortimer 1954, Plate 23, A & B), after a wind has been blowing steadily for some time. The epilimnion forms a wedge with the broad portion at the downwind end; the thermocline is correspondingly tilted and is narrower toward the downwind end; the metalimnic layers have been forced upwind and, in strong winds or in long lakes, lie at the surface at the upwind end (449 and Fig. 79 C & D, 283). The wind-driven circulation takes the form of a current running with the wind at the surface and a gradient (return) current running upwind, on top of the thermocline, in the lower part of the epilimnion.

There are two ways of looking at this state of affairs. Taylor (1931a) and Goldstein (1931) considered the stability of internal waves in superposed streams of fluid of differing densities. They were discussing not turbulence but the conditions under which a wave disturbance would grow despite the damping effect of the density gradient. When such waves grow and become unstable and "break" into eddies in the manner described by Mallock (1920) and Rosenhead (1931), the state we recognize as turbulence will ensue. Richardson's (1920,—not 1926 as on p. 256) approach was more directly related to modern ideas on turbulence. His criterion of stability is equivalent to the statement: if (a), the loss of energy by the turbulent eddies in doing work against gravity on the density gradient, is greater than (b), the supply of energy to the eddies from the mean flow, then turbulence will subside. If (b) is greater than (a), turbulence will increase. The term (a) is proportional to the density gradient (the first round-bracketed term on p. 255 should therefore not be squared), and the term (b) is proportional to the square of the shear, this being defined as the vertical velocity gradient. The criterion of stability turns out to be the same in the Taylor-Goldstein problem as in Richardson's; both are expressed as the non-dimensional ratio: (density gradient)/(shear)^2. When this ratio—the Richardson number—progressively decreases through the critical value, the passage from stable to unstable flow can, therefore, be described in two ways: either as a catastrophic growth of internal waves which "break" into large eddies, or as a sudden shift in the eddy spectrum from microturbulence toward macroturbulence. This shift is accompanied by a large increase in friction and mixing.

Application of this notion to the lake conditions described in the last paragraph but one produces the following hypothetical pattern. Shear, being greatest at the surface, breaks down any small density gradients which may have been present, thereby producing a well mixed epilimnion. As long as the shear of the return current is subcritical at the thermocline, this remains a slippery layer with little mixing across it; but if the shear becomes super-critical, macro-eddies give rise to large-scale mixing. Some of the mixed water drifts upwind with the current, thereby steepening the thermocline gradient at the downwind end. This process, which probably continues until the flow is just stabilized at the downwind

end, produces marked local differences in the shape and stability of the thermocline and gives rise to the fan-shaped distribution of isotherms in Figure 103.

When the wind is succeeded by a period of calm, the layers, which were displaced or newly created in the manner just described, become re-distributed by internal oscillations to new equilibria. This re-distribution will induce, as did the wind-driven displacement before it, horizontal flow at all levels, which will create instability wherever the Richardson number falls below the critical value. The final shape of the temperature profile at any point in the lake will, therefore, be the combined result of a number of events occurring during and after the wind disturbance and in widely separated regions of the basin.

This view of a lake in motion is not one which is stressed in Hutchinson's treatise, but it promises to be a fruitful one, and it has therefore been described here in some detail. Inevitably the main concepts in physical limnology have developed from single-station observations, but there is much still to be learned from detailed records of change in stability, shear, and turbulence in the basin as a whole. In the meantime, the following predictions may suggest possible solutions for some of the difficulties in the chapter on thermics. First, there is sufficient horizontal flow at all levels to meet the requirements on pp. 478 and 677.[1] Second, the thermocline exhibits a dual behaviour, depending on the value of the Richardson number, which perhaps explains the apparently conflicting observations on pp. 284, 474–5. Third, active mixing across the thermocline takes place only during wind- or seiche induced bursts of instability. This implies an intermittent and sometimes localized mechanism of hypolimnetic heating (466–71) and, further, suggests that the constancy of the "clinolimnetic" diffusion coefficient (472–75) is a statistical result of "an enormous number of observations" at one station and not a physical description of a transport mechanism in action at any one moment or place. This raises doubts about the validity of equation 33 (468) for, although it is "valid" when applied to the long-term mean conditions in Mendota (Fig. 141, p. 470), it is not therefore necessarily valid in the momentary states which make up that mean.

In the opening chapter of the chemical section the author gives a concise account of the sources of the major anions and cations in rain, lakes, and rivers, some of which are derived from the dissolution of rocks and some by re-cycling from the oceans. The main cations are those major metallic constituents of the earth's crust which do not form insoluble hydroxides or carbonates. There is a constant flux of these elements—sodium, potassium, calcium, and magnesium—from the crust to the ocean, and they are consequently present in varying proportions and concentrations in all waters. The main anions accompanying them are, with rare exceptions, bicarbonate, sulphate, and chloride, also in widely varying concentrations and proportions. Dispersed, often at extreme dilution, among these major constituents are many minor ones. Of the origin and fate of most of them little is known. Some are biologically active and play important although not always well understood roles in the complex biogeochemistry of water. Many problems remain to be solved and not among the minor constituents alone. Why, for instance, is the sulphate/chloride ratio much higher in rain and fresh waters generally than in the sea? Apart from industrial pollution, which is local, two explanations have so far been put forward (549), but they remain to be tested.

"A skillful limnologist can probably learn more about the nature of a lake from a series of oxygen determinations than from any other kind of chemical data" (575). The author illustrates this in a chapter which combines an account of the physics of solubility and transport across air/water interfaces with descriptions of concentration profiles observed at different seasons and in different lake types. Seasonal changes in the distribution of oxygen (592–609) and—in a complementary manner—of carbon dioxide (671–3) are geared, on the one hand, to the annual cycle of circulation and thermal stratification and, on the other, to the activities of plants, animals, and bacteria. These activities will be described in the second volume, and this presumably is why the author does not here discuss diurnal changes or review the comparisons which have been made between oxygen changes in submerged bottles with those in the surrounding water. The reader, however, is left with no illusions about the difficulty of applying experimental data to real lakes or, in particular, of assessing the effect of biological process and of estimating exchange across the highly variable interface between the air and a water column which cannot be isolated from horizontal exchange without substantially disturbing the system.

The factors controlling the interrelationships and equilibria between carbon dioxide, carbonic acid, bicarbonate, carbonate, and pH are presented with a clarity which gives no hint of the difficulty which the author must have had with the literature. Profiles of the various forms of carbon dioxide and of pH are presented for different lake types, but there are fewer examples to draw upon than for oxygen.

The final quarter of the volume is taken up with seven shorter chapters, all but one of which are concerned with the chemistry of quantitatively minor elements. It is well known, however, that some of these possess a biological importance out of all proportion to their concentration;

[1] Density currents (477) may also assume importance in a small, very sheltered basin. They certainly control distribution under ice, and the author is correct in regarding the "diffusion coefficients" tabulated on p. 476 as spurious.

sometimes—if they are plant nutrients—their importance is a direct result of their low concentration. Separate chapters are, therefore, devoted to the cycles of phosphorus, sulphur, silica, and nitrogen. These chapters introduce and elaborate many of the main themes of chemical limnology, and it seems almost irreverent to dismiss them in a few sentences. Phosphorus is regarded as the plant food most likely to become deficient and, therefore, to limit biological production in lakes. Radiophosphorus is the latest tool to be applied to studies of exchange within the lake system. Particular attention is paid to the geochemistry of iron. Although it is a very minor ionic constituent of waters containing oxygen, iron is relatively abundant in the lithosphere and in most lake sediments, and it exerts—through the ferric/ferrous system—a poising influence on the redox potential at interfaces between zones of oxidation and reduction (697–705), for example near the sediment/water interface or sometimes at the thermocline in stratified lakes. "No clear idea of the biochemical transformations in a lake can be gained without a consideration of the redox potential" (691), and to illustrate this the influence of various redox transformations of sulphur and nitrogen on lake metabolism is fully discussed. The cycle of silicon and its utilization by diatoms is somewhat less complex, although the precise form of this element in solution is still in doubt.

A number of minor elements are treated together in one chapter. It is a little surprising to find manganese among these. Although, like iron, it is only present in low concentrations in water containing oxygen, it is an important constituent of sediments, where the manganese/iron ratio is usually considerably higher than that in the lithosphere as a whole (804). It behaves in a similar manner to iron in a redox gradient. The occurrence in lake water of copper, zinc, aluminium, gallium, molybdenum, nickel, and cobalt is described. Of these only copper has been studied in any detail, and it is clear that much work remains to be done on the distribution and biological significance of these minor metallic elements. Isolated occurrences of other trace metals are noted but the distribution of the naturally radioactive species is more fully discussed, particularly in view of their possible use in dating lake sediments.

The present lack of knowledge of the nature of organic matter in lake waters is illustrated by the fact that the entire field can be adequately reviewed in a final chapter of twenty-five pages. Little progress can be made with the ubiquitous brown or yellow coloring matters until more is known of their origin, structure, and reactions—a complex but promising field of research. The occurrence of various vitamins and amino acids in waters and sediments is briefly discussed.

The relatively small space given here to the chemical half of this volume must not be allowed to obscure the fact that it is an authoritative, comprehensive, and most stimulating review of the wide field of chemical limnology. In a subject which embraces the chemistry of the earth and of living things, selection of material is inevitable, and it is not surprising that the author has laid most emphasis on the biogeochemistry of biologically important elements. But he has not excluded aspects of pure chemistry or physical chemistry where relevant, and we are promised that he will "revert to certain chemical matters" in the subsequent volume on lake biology. Its publication is most eagerly awaited.

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Marine Station
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Proceedings of the American Society of Limnology and Oceanography, Inc.

Minutes of the 21st Annual Meeting

Bloomington, Indiana

August 26, 1958

The meeting was called to order by President Leipper at 10:48 a.m.; 61 members were present. The minutes of the 20th Annual Meeting were approved as printed in Volume 3, No. 1 of LIMNOLOGY AND OCEANOGRAPHY.

Tellers Yentsch and Watson announced that 296 ballots had been cast in the annual election, and the following officers and members of the Editorial Board of the Society were declared duly elected:

President: William E. Ricker
Vice-President: Bostwick H. Ketchum
Secretary-Treasurer: George H. Lauff (3-yr. term)
Member-at-Large: John H. Ryther (3-yr. term)
Editorial Board (3-yr. terms):
John C. Ayers
Dayton E. Carritt
Joel W. Hedgpeth
Claude E. ZoBell

The Secretary reported that during 1958, 106 members have joined the Society of whom 99 are active members and 7 are associates. During the year 15 members have resigned, and 4 members apparently have moved without providing the Secretary with their change of address; 26 members have been suspended from the mailing list for non payment of dues. The total paid membership as of August 20th, 1958, is 819 of whom 23 are associate members and 13 are emeritus members. The number of members subscribing to the journal has increased to 783, which compares to the 715 subscribing members one year ago.

The number of library subscriptions to LIMNOLOGY AND OCEANOGRAPHY has increased, during the last year, from 147 to 217. The growth of the Society and of the number of libraries subscribing to the journal has been gratifying and has exceeded the estimates which were prepared at the time the publication of the journal was initiated.

The Treasurer presented the financial statement, a copy of which is appended, for the period January 1, 1957, to December 31, 1957, and January 1, 1958, to August 22, 1958. The Secretary-Treasurer further reported that in spite of the encouraging growth of the Society, the publication of the journal is still operating at a deficit. In 1957 a bill for deficit financing has been submitted to the National Science Foundation in the amount of $1,059.23. This deficit has resulted because of increasing costs of publication. If the publication of the journal were still costing the Society the same as Volume 1, there would be no deficit this year. It appears, however, that a deficit may also be anticipated for 1958, since an additional increase in cost of publication has applied to the publication of Volume 3. The sale of all the 1500 copies now being printed would be sufficient to cover the operating costs, but unless Society membership grows to this extent an increase in dues is inevitable.

The Secretary-Treasurer's reports were accepted by the Society.

David G. Frey, Editor of LIMNOLOGY AND OCEANOGRAPHY reported that, in contrast to last year when he was requesting manuscripts, he now has on hand enough to completely fill Volume 4. The present delay in publication is approximately 12 months. The editor

further reported that the manuscript quality was high and that the rejection rate has consequently been low. It was moved, seconded and passed that Dr. Frey be complimented on the high quality of the journal which has won international recognition.

Dr. Arthur D. Hasler reported on progress in the arrangements to invite the International Limnological Congress to meet in the United States in 1962. No final decision can be reached until the meeting in Austria in 1959. The preliminary plans are to hold the meeting in Madison, Wisconsin, with field trips to various sites in Canada and the United States. Dr. Hasler further reported that the committee had reached the conclusion that it would be necessary to raise approximately $100,000 for the purposes of the conference, $75,000 of this amount to be used for payment of travel expenses for foreign participants in the Congress.

The Secretary submitted a proposal received from Herbert Curl, Jr., suggesting that LIMNOLOGY AND OCEANOGRAPHY list translations of foreign papers possessed by the members which could be made available to the membership at cost of reproduction. It was moved, seconded, and passed that a committee be appointed to investigate the possibility of the Society acting as a clearing house for informal exchange of translations of foreign papers in aquatic science.

The President announced the appointment of the following members to committees or as representatives of the Society to serve through the indicated years.

Apparatus and Supplies:
John H. Ryther, Chairman, 1958
Charles S. Yentsch, 1960

Auditing Committee:
Herbert Graham, 1958
Arthur Miller, 1958

Identification Service Committee:
Joel Hedgpeth, Chairman, 1960

Nominating Committee:
David C. Chandler, Chairman, 1958
David G. Frey, 1958
Carl L. Hubbs, 1958

National Research Council:
Lionel A. Walford

The President announced that the 22nd Annual Meeting would be held at Pennsylvania State College in 1959 and that the 23rd Annual Meeting would be held at Oklahoma A & M College in 1960.

The President also announced that the Board of Directors had recommended that hereafter the vice-president of the Society be the program chairman for the annual meetings. Mr. Charles S. Yentsch suggested from the floor that a symposium on zooplankton ecology would be appropriate for the meeting next year.

The meeting moved a vote of thanks to David G. Frey, Local Chairman, for the meeting at Bloomington. On the motion of President Dale F. Leipper, the retiring Secretary-Treasurer was given a rising vote of thanks for his services during the six years of his tenure of office.

The meeting was adjourned at 11:37 a.m.

Respectfully submitted,
BOSTWICK H. KETCHUM
Secretary-Treasurer

Financial Statement

	Jan. 1, 1957 to Dec. 31, 1957	Jan. 1, 1958 to Aug. 22, 1958
Balance on Hand	$3,849.06[1]	$6,715.16[2, 3]
Receipts		
Dues	7,120.55[2]	3,625.50
Library Subscriptions	2,729.63[3]	1,556.87
Special Publications	5.75	3.70
Reprint Sales	1,530.34	1,125.42
Contributions (Appar. & Sup. Publ.)	202.00	—
National Science Foundation	1,369.97	—
Special Meeting	34.32	—
Pacific Section—return of funds	138.07	—
Interest	231.44	107.07
Proof Correction Charges	35.25	—
Miscellaneous	—	6.00
Total Receipts	$17,246.38	$13,139.72
Expenditures		
Addressograph Service	67.44	58.03
Printing	276.71	79.13
Postage	185.36	46.19
Secretarial Service	166.37	133.20
Travel	408.89	None
Contributions		
AIBS	100.00	100.00
NRC	25.00	25.00
Pacific Section	—	55.89
Miscellaneous	35.72	16.80
LIMNOLOGY AND OCEANOGRAPHY		
Manufacture	7,366.96[4]	6,701.43
Address and Mail	245.99	226.51
Reprints	1,230.04	1,124.59
Secretarial (Bus. Mgr.)	332.74	—
Editorial Board Expenses	50.00	50.00
Miscellaneous	40.00	24.95
Total Expenditures	$10,531.22	$8,641.72
Balance	6,715.16	4,498.00[5]
Balance on Hand		
Savings Account	6,273.50	4,305.01
Checking Account	441.66	192.99
	$6,715.16	$4,498.00

[1] Includes $1,739.90 of 1957 dues and subscriptions paid in 1956.
[2] Includes $2,600.00 of 1958 dues paid in 1957.
[3] Includes $936.50 of 1958 subscriptions paid in 1957.
[4] Includes $649.00 partial payment for Volume III, No. 1.
[5] Includes $134.50 of 1959 dues and subscriptions paid in 1958.